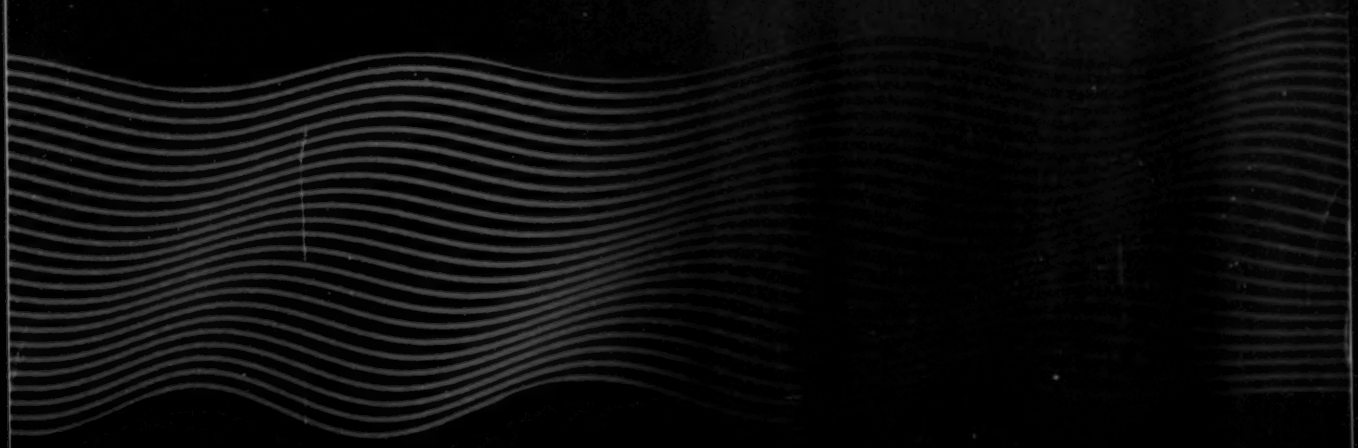
National Research Council Canada

Conseil national de recherches Canada

NRC · CNRC

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques



ISSN 0706-652X / CJFSDX 55(12) 2533–2710 (1998)

The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy: The Journal publishes original research articles, perspectives (syntheses, critiques, re-evaluations), discussions (comment and reply), and rapid communications. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results. The Journal encourages papers that lead from clearly stated purpose or rationale and from testable hypotheses, concepts, or questions to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. The Journal discourages papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); only confirm previously established principles; or apply standard techniques without breaking new methodological ground.

Manuscripts for publication should be submitted to the Editors, Canadian Journal of Fisheries and Aquatic Sciences, Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 ext. 2646; fax: 519-767-9798; e-mail: cjfas@uoguelph.ca).

Submissions in either English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. NRC accepts no responsibility for statements or opinions expressed by a contributor. Acceptance of an advertisement, announcement, or other material does not imply endorsement by either the *Journal*'s Editors or NRC. The use of proprietary names does not imply endorsement of the product or company.

Correspondence concerning accepted manuscripts and corrected proofs should be sent to NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Instructions to Authors are published once a year in the first issue of each volume. Copies are available from NRC Research Press or from our Web site. The **Publication Policy** of NRC Research Press is also available at our Web site:
http://www.nrc.ca/cisti/journals/rj.html

Microfilm: Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, U.S.A.

U.S. periodical postage paid at Champlain, N.Y., and at additional mailing offices. Attention U.S. POSTMASTER: Send address changes to **Canadian Journal of Fisheries and Aquatic Sciences**, c/o USACAN Media Distribution Center, P.O. Box 2888, Plattsburg, NY 12901, U.S.A.

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, et *Journal of the Fisheries Research Board of Canada* 1938–1979. Le *Journal* paraît tous les mois, formant ainsi un volume de 12 numéros, et offre en plus jusqu'à deux suppléments par année.

Politique éditoriale : On publie, dans le Journal, des articles rendant compte de recherche originale, des perspectives (synthèses, critiques et réévaluations), des discussions (commentaires et réponses) et des communications rapides. Les documents peuvent porter sur les cellules, organismes, populations, communautés, écosystèmes ou processus qui affectent les systèmes aquatiques. Ils peuvent relever de divers domaines y compris la biologie et l'écologie des organismes marins et d'eau douce, la limnologie, l'océanographie, la physiologie, la toxicologie, la génétique, l'économie, la pathologie et la gestion. On accorde la préséance aux articles qui contribuent à la compréhension de phénomènes observés et à l'interprétation de résultats expérimentaux. On invite les auteurs à soumettre des articles ayant des objectifs précis ou relevant d'hypothèses, de concepts ou de questions vérifiables et se terminant par de solides conclusions ou d'utiles synthèses. Ces articles enrichissent, changent, mettent en question ou réorientent les connaissances acquises sur divers aspects des sciences aquatiques. On décourage toutefois la soumission d'articles simplement descriptifs (à moins qu'il ne s'agisse de nouvelles disciplines), d'application très limitée (applicables à une seule année, une seule région ou un seul taxon, portant sur un unique composé chimique, etc.); d'articles qui ne font que reprendre les principes énoncés dans des articles précédents; et d'articles rendant compte de l'application de normes sans gain de méthodologie.

Les auteurs voudront adresser leurs **manuscrits** aux directeurs scientifiques, Journal canadien des sciences halieutiques et aquatiques, Département de Zoologie, University of Guelph, Guelph, ON N1G 2W1, Canada (519-824-4120 poste. 2646; télécopieur : 519-767-9798; adresse électronique : cjfas@uoguelph.ca).

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à.-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le CNRC ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations qui pourrait faire ce dernier. La publication d'annonces publicitaires, d'avis et autres n'implique pas l'endossement de leur contenu par les directeurs du *Journal* ou du CNRC. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

La correspondance ayant trait aux manuscrits acceptés et les **épreuves corrigés** doivent être envoyées aux Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Recommandations aux auteurs sont publiés une fois par année dans le premier numéro de chaque volume. Des copies, ainsi que la **Politique de publication**, sont disponibles auprès des Presses scientifiques du CNRC ou au site Web :
http://www.nrc.ca/cisti/journals/rj.html

Microfilms : On peut acheter sur microfilms de 16 ou 35 mm tous les numéros depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, É.-U.

This journal is indexed or abstracted in / Ce journal est signalé ou résumé dans
Aquatic Sciences and Fisheries Abstracts, Biological & Agricultural Index, CAB Abstracts (Centre for Agriculture and Biosciences), Chemical Abstracts, Current Awareness in Biological Sciences, Current Contents, FAO Freshwater and Aquaculture Contents Tables, FAO Marine Science Contents Tables, GEOBASE – Geo Abstracts, Meteorological and Geoastrophysical Abstracts, Oceanic Abstracts, Science Citation Index, Biological Abstracts, Environment Abstracts, Environmental Periodicals Bibliography, GEOREF, Life Sciences Collection, ABSEARCH, and PASCAL Database

Volume 55, Number 12, December 1998

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 55, numéro 12, décembre 1998

Journal canadien des sciences halieutiques et aquatiques

Publié par le Conseil national de recherches du Canada

Editors / directeurs scientifiques John C. Roff and Moira M. Ferguson

Assistant to the Editors / adjointe aux directeurs scientifiques **Holly Foster**

Associate Editors / directeurs scientifique associés

D. Boisclair, *Université de Montréal*
U. Borgmann, *Environment Canada, Burlington*
S.E. Campana, *DFO/MPO, Dartmouth*
B. de Young, *Memorial University of Newfoundland*
D.G. Dixon, *University of Waterloo*
A.E. Dizon, *National Marine Fisheries Service, La Jolla, Calif.*
J.J. Dodson, *Université Laval*
J.A. Downing, *Iowa State University*
K.T. Frank, *DFO/MPO, Dartmouth*
F.A. Huntingford, *University of Glasgow*
J.A. Hutchings, *Dalhousie University*
G.S. Jamieson, *DFO/MPO, Nanaimo*
B. Jonsson, *Norwegian Institute for Nature Research, Oslo, Norway*
L. Legendre, *Université Laval*
R.M. Peterman, *Simon Fraser University*
E.E. Prepas, *University of Alberta*
T.P. Quinn, *University of Washington, Seattle, Wash.*
R.D. Robarts, *Environment Canada, Saskatoon*
P.F. Sale, *University of Windsor*
D.W. Schindler, *University of Alberta*
S.J. Smith, *DFO/MPO, Dartmouth*
W.G. Sprules, *University of Toronto*
R.J. Thompson, *Memorial University of Newfoundland*
C.J. Walters, *University of British Columbia*
R.D. Ward, *CSIRO Division of Fisheries, Australia*
C.M. Wood, *McMaster University*

NRC Research Press / Presses scientifiques du CNRC

Editor-in-chief / directeur général **Bruce P. Dancik**
Assistant Editor-in-chief / directeur général adjoint **Iain E.P. Taylor**

Journals Program / Programme des revues

(Fax / télécopieur : 613-952-7656; e-mail / adresse électronique : research.journals@nrc.ca;
URL: http://www.nrc.ca/cisti/journals/)

Director / directrice **Aldyth Holmes**
Business Manager / gestionnaire des affaires **Paul McClymont**
Manager, Journals Program / gestionnaire, Programme des revues **Susan R. Strahlendorf**
Senior Publication Officer / agente principale de publication **Jennifer Douglas**
Publication Officer / agente de publication **Jennifer McColl (613-993-4500)**
Advertising / annonces publicitaires **Judy Heyman (613-993-0151)**
Reprints / tirés à part **Roxanne Landriault (613-990-2254)**
Subscriptions / abonnements **Helen Goulet (613-993-9084)**

© National Research Council of Canada 1998. World rights reserved.
No part of this publication may be reproduced, stored, or transmitted in any form or by any means, without the written permission of the publisher, except as stated below.

The National Research Council of Canada grants **permission*** to individuals to make single copies of articles for personal use. Any person may reproduce short excerpts from articles in the journal for any purpose that respects the moral rights of authors, provided that the source is fully acknowledged. As a courtesy, the consent of authors of such material should be obtained directly from the author.

Authorization to reproduce items for other than personal use, as stated above, is granted by the National Research Council of Canada provided that the copyright fee of $7.00 per copy is paid directly to the Copyright Clearance Center (CCC) Transactional Reporting Service, 222 Rosewood Drive, Danvers, MA 01923, U.S.A. 0706-652X/98 $7.00.

*The above permission does not extend to other kinds of copying, such as copying for general distribution, for advertising, or promotional purposes, for creating new collective works, or for resale. For such copying, arrangements must be made with the publisher, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

© Conseil national de recherches du Canada 1998. Tous droits réservés.
Il est interdit de reproduire, de sauvegarder ou de transmettre quelque partie de la présente publication dans quelque format ou de quelque façon sans le consentement écrit de l'éditeur, à l'exception des conditions suivantes.

Le Conseil national de recherches du Canada accorde aux particuliers le droit de faire des copies individuelles pour leur usage personnel. Toute personne peut reproduire de courts extraits des articles de la Revue pour autant que les droits moraux de l'auteur soient respectés et que la mention de provenance soit clairement indiquée. Il est de convenance de demander le consentement de l'auteur avant de faire mention de son travail.

On obtiendra l'autorisation de reproduire des articles à d'autres fins que l'usage personnel (tel qu'on l'a décrit ci-dessus) auprès du Conseil national de recherches du Canada pour autant que des redevances de droits d'auteurs de 7,00 $/copie soient versées au Copyright Clearance Center (CCC) Transactional Reporting Service, 222 Rosewood Drive, Danvers, MA 01923, U.S.A. 0706-652X/98 7,00 $.

*La permission ci-dessus ne s'applique pas à la reproduction à grande échelle, telle que la reproduction aux fins de distribution générale, publicitaire ou promotionnelle, de compilation de nouveaux ouvrages collectifs ou de revente. Dans de tels cas, il faudra ratifier une entente particulière avec l'éditeur, le Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Subscription information

The *Canadian Journal of Fisheries and Aquatic Sciences* (ISSN 0706-652X) is published monthly by the National Research Council of Canada. 1999 annual subscription rates (second class postage) for Canada are $578CAN institutional and $182CAN personal, for US & foreign $578US institutional and $192US personal. For air mail add $150US to foreign rate. Canadian customers please include 7% GST (business no. 12149 1807 RT 0275). Subscriptions are entered for the calendar year. Remittances should be made payable to the Receiver General for Canada credit NRC. Price for regular single issues: institutional, $75.00; personal, $25.00. Supplements will be priced separately. Special rates apply to members of Canadian scientific and engineering societies if they subscribe through their respective societies.

There are no refunds on cancelled subscriptions once delivery has begun. Claims for missing issues should be made within four months (N. America) or six months (outside N. America) following the date of publication. The publisher expects to supply missing issues only when losses have occurred in transit and when the reserve stock will permit. For change of address and subscription enquiries: Subscription Office, NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada; tel: 613-993-9084; fax: 613-952-7656; e-mail: research.journals@nrc.ca.

Microform backfiles are available from UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, U.S.A., and Micromedia Ltd., 20 Victoria St., Toronto, ON M5C 2N8, Canada.

The 1998 issues of the *Canadian Journal of Fisheries and Aquatic Sciences* are available on the Web. Pricing information can be found at

http://www.nrc.ca/cisti/journals/

Renseignements sur l'abonnement

Journal canadien des sciences halieutiques et aquatiques (ISSN 0706-652X) est une publication mensuelle du Conseil national de recherches du Canada. Le prix de l'abonnement annuel au Canada (courrier de deuxième classe) est de 578 $CAN pour les organismes et de 182 $CAN pour les particuliers. À l'étranger (y compris les É.-U.), le prix de l'abonnement est de 578 $US pour les organismes et de 192 $US pour les particuliers. L'expédition par avion exige des frais de 150 $US en sus du prix d'abonnement à l'étranger. Les clients du Canada doivent ajouter la TPS de 7% (numéro d'entreprise 12149 1807 RT 0275). Les abonnements sont pour l'année civile. Tout paiement doit être adressé au Receveur général du Canada, crédit du CNRC. Le prix par numéro est de 75 $ pour les organismes et de 25 $ pour les particuliers. Le prix des hors-série varie. Les membres des sociétés canadiennes de sciences et de génie bénéficient de taux préférentiels en s'abonnant via leurs sociétés respectives.

Aucun remboursement ne sera accordé ni aucune annulation acceptée une fois que les livraisons auront commencé. Les réclamations de numéros manquants devront être soumises dans les quatre mois (Amérique du Nord) ou dans les six mois (à l'extérieur de l'Amérique du Nord) suivant la date de publication. L'éditeur ne fournira de numéros manquants que si le document a été perdu pendant l'expédition et que si le stock le permet. Adressez tout changement d'adresse ou toute question quant à l'abonnement au : Bureau des abonnements, Presses scientifiques du CNRC, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada; téléphone : 613-993-9084; télécopieur : 613-952-7656; adresse électronique : research.journals@nrc.ca.

On peut obtenir les fichiers rétrospectifs sur **microforme** auprès de UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, É.-U., et auprès de Micromedia Ltée, 20 rue Victoria, Toronto, ON M5C 2N8, Canada.

Les numéros de 1998 de *Journal canadien des sciences halieutiques et aquatiques* sont accessibles sur le Web. On trouvera des renseignements sur les tarifs à

http://www.nrc.ca/cisti/journals/rjfr.html

RAPID COMMUNICATION / COMMUNICATION RAPIDE

Is solar radiation responsible for declines in marine survival rates of anadromous salmonids that rear in small streams?

Carl Walters and Bruce Ward

Abstract: There have been profound declines in marine survival rates of steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), chinook salmon (*O. tschawytscha*), and Atlantic salmon (*Salmo salar*) since the mid-1980s, and these declines have been particularly acute in sunny regions. We suggest that the problem may originate in freshwater with radiation (e.g., UV-B) damage to metabolic machinery that is expressed during stressful periods of smolting and ocean entry and that progressively worse damage may soon appear as reduction in freshwater survivals as well. This hypothesis can be tested quickly by management agencies by comparing survival rates of hatchery-reared fish with and without radiation protection during rearing.

Résumé : Nous observons depuis le milieu des années 80 des baisses graves du taux de survie en mer du saumon arc-en-ciel (*Oncorhynchus mykiss*), du coho (*O. kisutch*), du quinnat (*O. tschawytscha*) et du saumon atlantique (*Salmo salar*). Ces baisses sont particulièrement marquées dans les régions ensoleillées. Nous pensons que le problème trouve son origine en eau douce, le rayonnement (p. ex. les UV-B) causant des dommages métaboliques qui s'expriment pendant les périodes de stress que sont la smoltification et l'entrée en mer, et que des dommages de plus en plus graves pourraient se manifester bientôt sous la forme d'une réduction de la survie en eau douce également. Cette hypothèse peut être vérifiée rapidement par les organismes de gestion : il suffirait de comparer les taux de survie de poissons d'élevage qui seraient protégés ou non du rayonnement pendant le grossissement.

[Traduit par la Rédaction]

Geographic and temporal patterns in survival

Declines in marine survival rates and recruitment rates per spawner have severely impacted steelhead, coho, chinook, and Atlantic salmon populations throughout the northern hemisphere, from Britain to California (Fig. 1). Many populations in California, Oregon, and Washington are or will soon be listed as endangered. There were major disruptions in B.C. commercial and sport fisheries in 1998 to protect declining coho and steelhead populations. Meanwhile, some lake- and ocean-rearing salmons like sockeye (*O. nerka*) and pink (*O. gorbuscha*) exhibited good survival during the late 1980s, as did coho in Alaska (Hare et al. 1998). Marine survival rates of many stocks of chinook salmon (*O. tschawytscha*) have declined severely but over a longer time period and for both stream- and ocean-rearing life-history types (Beamish et al. 1997). Despite severe declines in harvest and high smolt abundances, most Canadian Atlantic salmon stocks (except Newfoundland) have shown some decline in adult abundance (Anonymous 1998).

For B.C. coho, where we have data over a variety of freshwater-rearing situations, there is a disturbing correlation between sunlight and the declines. We see differences in trends between interior and coastal populations (declines have been much more severe and started earlier for interior stocks rearing in relatively sunny, rain-shadow areas), southern and northern stocks (southern stocks started declining sooner than stocks from more northerly, wetter regions where very low survivals have been seen only after 1995), and cloudy and sunny regions within the southwestern B.C. coastal region (higher recent survivals in Fig. 1 are for stocks from rainy areas on the west coast of Vancouver Island and the upper Fraser Valley, while survivals are lowest for stocks that rear in the rain-shadow region of eastern Vancouver Island). Trends are similar in wild and hatchery populations. B.C. steelhead sport catch statistics show similar spatial patterns and trends. Mean survival rates over coho stocks from the data in Fig. 1 for 1989–1994 were ordered by region from wet to dry (using mean 1961–1990 rainfall, stations indicated), and an index of change in survival rate was calculated (mean survival for 1989–1994 divided by mean survival for 1973–1988; Table 1).

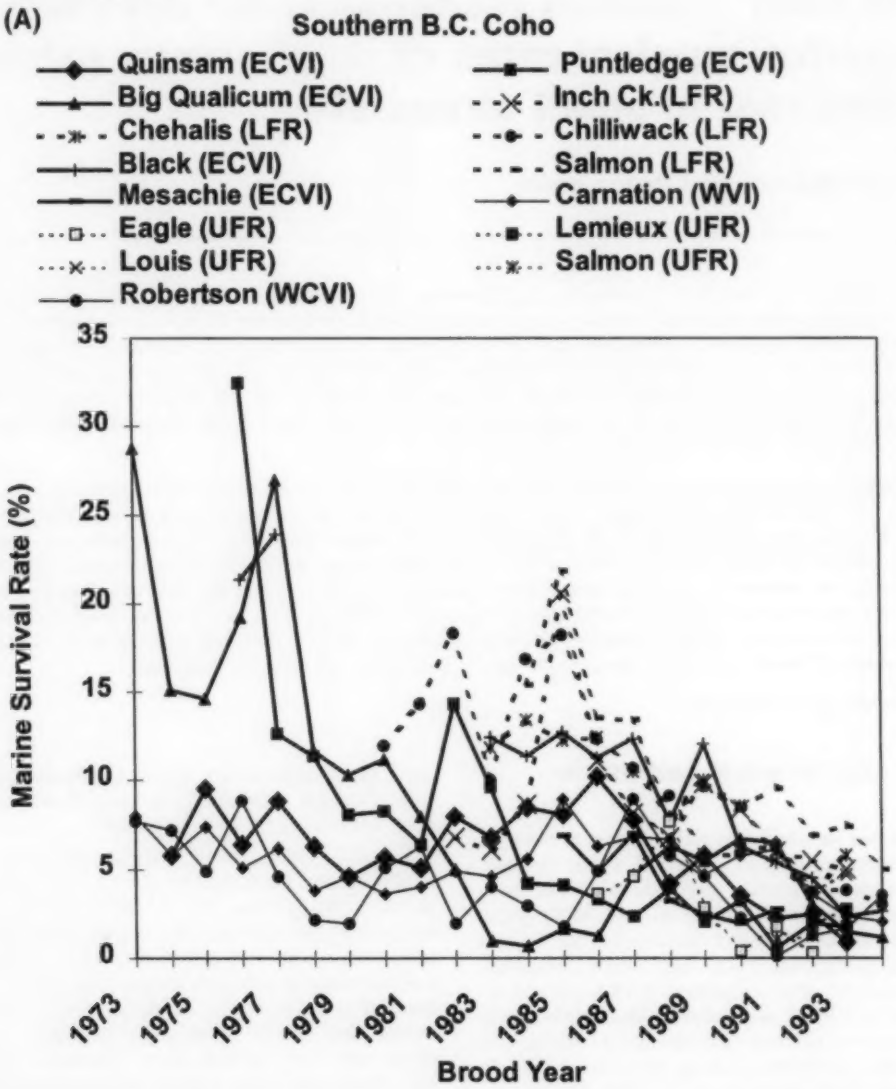
Received October 13, 1998. Accepted December 1, 1998. J14824

C. Walters[1] **and B. Ward.** Fisheries Centre, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

[1]Author to whom all correspondence should be addressed. e-mail: walters@fisheries.com

© 1998 NRC Canada

Fig. 1. Trends in apparent marine survival rate estimated from coded wire tag returns (B.C. coho), recruits/spawner (R/S) ratios (east coast Atlantic salmon), and direct fence counts of smolts and adults (steelhead). For coho, WCVI = west coast Vancouver Island stock, ECVI = east coast Vancouver Island, LFR = lower Fraser River, UFR = upper (interior) Fraser River, NC = north coast. Sources: coho, Canadian Department of Fisheries and Oceans, PSARC reports; steelhead, Cramer et al. 1998; Atlantic salmon, G. Chaput, DFO Moncton, personal communication.

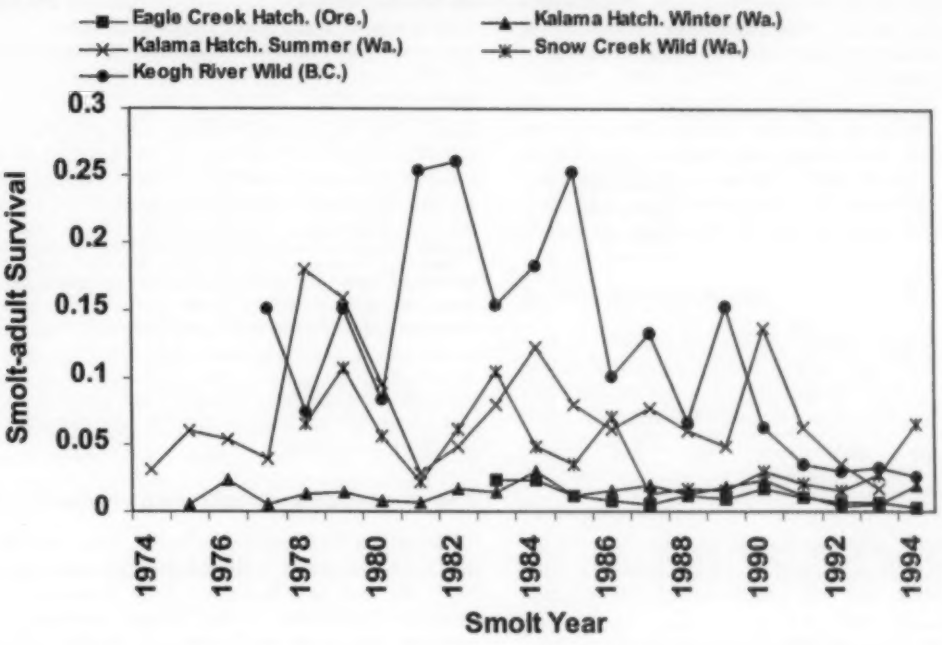


Regions are ordered in terms of relative decrease in survival rate; however, the west coast of Vancouver Island (WCVI) had lower survival rates in earlier years so fared better than the lower Fraser River (LFR) only in terms of relative decrease in survival. The differences in mean survival rate are highly significant (one-way ANOVA, years as repeated measures, $F_{3,11} = 9.35$, $P < 0.002$), but the differences in survival ratios are not ($F_{3,8} = 2.84$, $P = 0.11$). Curiously, wild coho stocks from Puget Sound (climatic conditions similar to LFR) have shown considerably higher marine survival rates than those from the adjoining Georgia Strait but with similar downward trends (Beamish et al. 1997; W. Tweit, Washington Department of Fish and Wildlife, unpublished data). Another word of caution is that the east coast Vancouver Island (ECVI) data include one stock (Mesachie) with juveniles that rear in a lake and hence might not be expected to be exposed to radiation patterns as severe as those experienced by stream-reared juveniles.

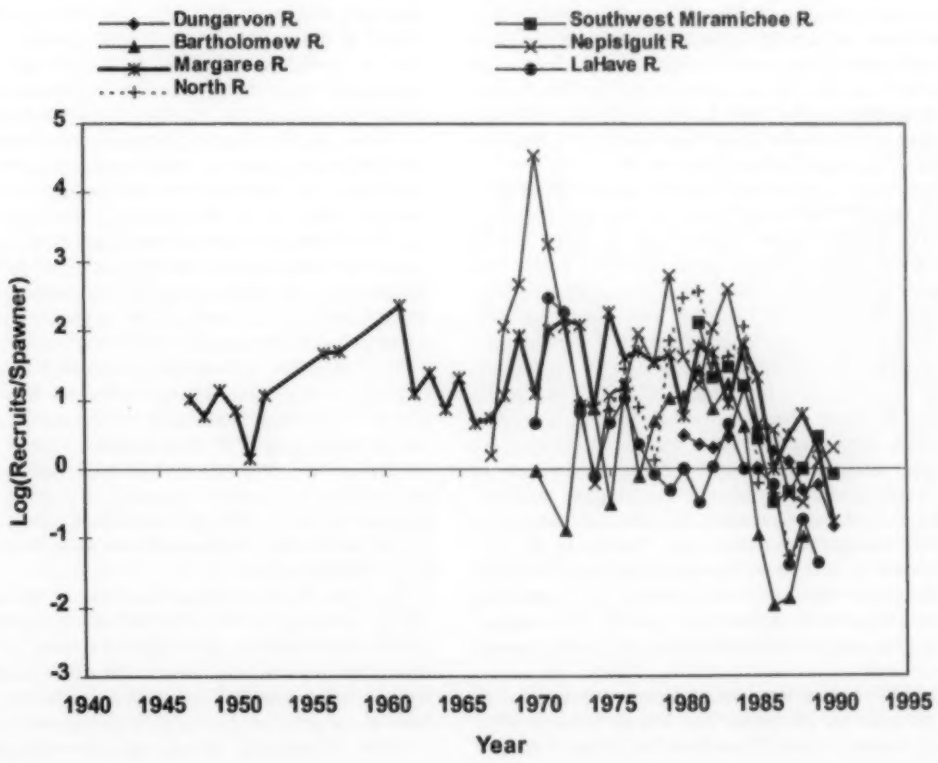
For Atlantic salmon, temporal patterns in direct measures of marine survival rate (as opposed to the overall recruits/spawner trends in Fig. 1) also show geographical differences suggestive of a climatic effect: survival rates for Newfoundland stocks (wet region) declined in the late 1980s but recovered during the 1990s, while survival rates for Quebec

© 1998 NRC Canada

(B) Pacific steelhead stocks

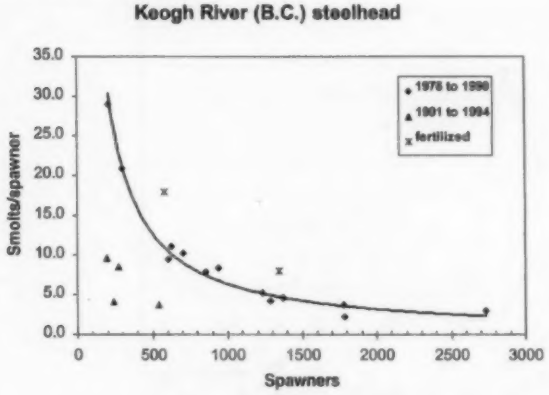


(C) New Brunswick Atlantic salmon



© 1998 NRC Canada

Fig. 2. Recent declines in freshwater survival rates of steelhead trout in the Keogh River, B.C., suggest that earlier declines in marine survival rates are now being followed by freshwater impacts as well (fertilized = smolt yield from years of nutrient addition to the stream).



and New Brunswick (drier regions) declined but have not recovered (Chaput 1997; Chaput et al. 1998). However, even Newfoundland stocks had very low returns in 1997 (Dempson et al. 1998).

Only two major B.C. sockeye populations have collapsed in recent years. The Rivers Inlet, Owikeeno Lake, population is noted for having among the smallest of smolts and for being the only major stock with juveniles that rear only in the top few metres of the lake water column; the lake is extremely turbid with glacial flour (Hyatt et al. 1989). Marine survival rates apparently started declining in the early 1980s in conjunction with a decreasing trend in freshwater flow and smolt size (C. Wood, DFO, personal communication). However, the nearby Long Lake population showed a similar decline, and that lake is not highly turbid. A common "marine effect" is suggested for both stocks.

Patterns are more complex for chinook salmon, which have both ocean-rearing ("fall") and freshwater-rearing ("spring–summer") life-history types. Some fall hatchery stocks showed severe survival declines during the late 1970s, and survivals have remained low since then. In contrast, spring–summer stocks from the B.C. interior and upper Columbia River also had relatively poor recruit/spawner performance during the mid-1970s but then had a period of higher survival, followed in the early to middle 1980s with severe declines similar to those shown for other species in Fig. 1 (Bradford 1994; Deriso et al. 1996). Analytical methods for recruit/spawner analysis developed by Deriso et al. appear to effectively separate effects of changes in "marine survival" from effects of freshwater changes in adult abundance and various water management (dams, etc.) factors in the Columbia. Considering that there was an earlier period of low survivals, the recent declines could as easily be interpreted as part of a longer term regime shift pattern (Hare et al. 1998) rather than a novel response to current environmental conditions.

There are hints that the survival problem is "spreading" to freshwater, at least for steelhead. The Keogh River in B.C. first showed marine survival declines but in the last few years has also had very low egg–smolt survival rates (Fig. 2) that cannot be explained by any obvious changes in freshwater habitat conditions.

Table 1. Climate and smolt-to-adult survival (S) of coho stocks for British Columbia in wet to dry regions and survival before 1988 compared with the last 5 years of returns.

Climate (month.year, days of rain (stations))	Region	Mean S (%)	S_{recent}/S_{older}
3.3, 202 (Tofino)	WCVI	3.17	0.59
1.7, 190 (Agasiz)	LFR	6.51	0.53
1.1, 167 (Nanaimo)	ECVI	3.58	0.38
0.3, 102 (Kamloops)	UFR	2.14	0.41

Note: S_{recent}, average survival rate from 1989–1995; S_{older}, average survival rate from 1973–1988. Survival data from Simpson et al. (1997); climate data from Environment Canada (www.cmc.ec.gc.ca/climate/normals/eprovwmo.htm).

The metabolic impairment hypothesis

Marine survival patterns as in Fig. 1 are usually assumed to reflect changes in marine environments (Beamish et al. 1997; Beamish and Bouillon 1995). However, the striking common denominator is not marine conditions but rather extended freshwater stream rearing. Further, differences associated with photoperiod and cloudiness suggest an atmospheric effect. Over a wide range of freshwater flow and thermal regimes, there is a striking correlation between the declines and temporal changes in indices of radiation (ozone depletion at ground level (Tarasick et al. 1996); UV-B penetration in freshwater lakes (Schindler et al. 1996)). A connection between radiation and survival would not be surprising, considering growing evidence of UV radiation impacts on aquatic productivity in general (e.g., Bothwell et al. 1994; Zagarese and Williamson 1994), as well as direct physiological effects on fish ranging from simple sunburn (McArdle and Bullock 1987) to suppression of immune responses (Salo et al. 1998) and egg mortality (Williamson et al. 1997). We can rule out the possibility that radiation impacts have been important but have acted through effects on productivity of marine-rearing environments; such effects should have had at least as much impact on chum, pink, and sockeye as on the stream-rearing species.

The metabolic impairment hypothesis is that increasing exposure to radiation during freshwater rearing first causes metabolic damage that results in increased mortality during the stressful period of smoltification, ocean migration, and adaptation to salt water. If this hypothesis is correct, what we measure as "marine" mortality is actually a symptom of exposure to stress during freshwater rearing. At higher dose levels, increasing metabolic effects should result in mortality in freshwater as well.

The only direct evidence we have of abnormal mortality during smolting is for coho in the Keogh River. Sawada (1993) found surprisingly high (up to 50%) mortality during migration from rearing sites to the river mouth; this mortality was independent of travel distance, hinting it was not related to cumulative exposure to factors such as predators.

Other mechanisms besides radiation damage could cause

© 1998 NRC Canada

delayed mortality in early ocean life following freshwater stress. Increased rearing temperatures, reduced insect food densities, etc., could result in juveniles having lower energy reserves for migration and marine predator avoidance. That is, there could be a whole syndrome of impacts due to changes in freshwater climatic factors. However, we can rule out the possibility that delayed mortality is due to general effects of degradation in freshwater-rearing habitats unrelated to particular factors like radiation; most of the declining trends in Fig. 1 are for hatchery stocks that are not subject to such effects (except during smolt migration from hatchery to sea).

If the metabolic impairment hypothesis is correct, marine survival rates will not recover even if ocean conditions return to "normal." However, there is some reason to hope for eventual recovery if the adults now surviving are treated as precious and are protected from harvesting and further habitat damage. There are species-specific differences in susceptibility to UV-B radiation (Blazer et al. 1997), indicating that natural selection on factors such as skin pigmentation can eventually result in fish better able to cope with current conditions.

Tests that we pray will fail

There are at least two immediate ways for management agencies with hatchery and data resources to test the metabolic impairment hypothesis:

1. Experimental: Conduct paired comparisons, using hatchery stocks, of marine survival rates for fish reared with and without UV-B protection. This would require tagging and rearing large numbers of smolts for each treatment group and effective sampling of adult returns for tagged fish. It is well within the capability of B.C. hatchery programs considering the large number of fish already being tagged for catch composition and hatchery performance evaluations.
2. Comparative: Develop more detailed and extensive comparative studies using the variety of time series now being collected. Such comparisons should reveal spatial differences due to variation in factors that affect radiation exposure, such as dissolved organic matter concentration (DOC, humic acids, etc.) in rearing streams and also temporal variation correlated with indices of radiation loading (cloudiness, etc.). If we are correct that impacts are now starting to appear in freshwater, declines should be starting to appear in survival rates for stream-rearing life stages of non-anadromous populations. Declines should also be starting to appear in more northerly (e.g., Alaskan) populations, and these declines should be persistent.

Note here that we do not recommend detailed process research (radiation effects, etc.) as a high immediate priority; considering the many pathways through which effects could occur, such studies could neither prove nor disprove existence of an overall effect. However, there is one type of detailed study that could be worthwhile: a critical part of our argument is that marine survival effects should appear very shortly after ocean entry. All we know now is that fish enter the ocean and "soon" disappear, probably during the first summer–fall of ocean rearing. It may be possible in some situations (e.g., Georgia Strait) to measure ocean dispersal and densities more accurately and hence determine whether the mortality is occurring as early as we suspect.

If the immediate tests do not fail, in the sense that strong radiation effects are found in the next few years, there will need to be some major changes in research priorities concerning the relationship between salmonids and the marine environment. In particular, studies will need to focus much more carefully on conditions faced by the fish during early ocean life, on the mechanisms of physiological damage, and on options for mitigating effects during freshwater rearing.

Acknowledgements

Jessica Bratty and Robert Ahrens, both from The University of British Columbia, worked hard to obtain references and data and to help develop the ideas. Brian Dempson, DFO, provided information on recent changes in Atlantic salmon stocks.

References

Anonymous. 1998. Atlantic salmon abundance: overview for 1997. Canadian Department of Fisheries and Oceans, Stock Status Report DO-02.

Beamish, R.J., and Bouillon, D.R. 1995. Marine fish production trends off the Pacific coast of Canada and the United States. *Edited by* R.J. Beamish. Can. Sp. Pub. Fish. Aquat. Sci. 121. pp. 585–591.

Beamish, R.J., Mahnken, C., and Neville, C.M. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale natural shifts in the productivity of the marine environment. ICES J. Mar. Sci. **54**: 1200–1215.

Blazer, V.S., Fabacher, D.L., Little, E.E., Ewing, M.S., and Kocan, K.M. 1997. Effects of ultraviolet-B radiation on fish: histologic comparison of a UVB-sensitive and a UVB-tolerant species. J. Aquat. Animal Health, **9**: 132–143.

Bothwell, M.L., Sherbot, D.M.J., and Pollock, C.M. 1994. Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. Science (Washington), **265**: 97–100.

Bradford, M.J. 1994. Trends in the abundance of chinook salmon (*Oncorhynchus tshawytscha*) of the Nechako River, British Columbia. Can. J. Fish. Aquat. Sci. **51**: 965–973.

Chaput, G.J. 1997. Proceedings of a workshop to review conservation principles for Atlantic salmon in eastern Canada. Can. Dep. Fish. Oceans, Can. Stock Assessment Proc. Ser. 97/15.

Chaput, G.J., Allard, J., Caron, F., Dempson, J.B., Mullins, C.C., and O'Connell, M.F. 1998. River-specific target spawning requirements for Atlantic salmon (*Salmo salar*) based on a generalized production model. Can. J. Fish. Aquat. Sci. **55**: 246–261.

Cramer, S.P., Cramer, D.P., Willis, C.F., Shrier, F., Vigg, S.C., Phillips, C., Hawksworth, J.T., Welty, J.J., Montagne, R., and Reininga, K. 1998. Synthesis and analysis of the Lower Columbia steelhead initiative. Special Report to National Marine Fisheries Service, Portland, Oregon.

Dempson, J.B., Reddin, D.G., O'Connell, M.F., Helbig, J., Bourgeois, C.E., Mullins, C., Porter, T.R., Lilly, G., Carscadden, J., Stenson, G.B., and Kulka, D. 1998. Spatial and temporal variation in Atlantic salmon abundance in the Newfoundland–Labrador region with emphasis on factors that may have contributed to low returns in 1997. DFO Canadian Stock Assessment Secretatiat, Res. Doc. 98/114.

© 1998 NRC Canada

Deriso, R.B., Marmorek, D., and Parnell, I. 1996. Retrospective analysis of passage mortality of spring chinook of the Columbia River. Chapter 5 *In* Plan for analyzing and testing hypotheses (PATH) final report on retrospective analyses. *Edited by* D. Marmorek. ESSA Technologies, Vancouver, B.C.

Hare, S.R., Mantua, N.J., and Francis, R.C. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries, **21**(1): 6–14.

Hyatt, K.D., Rankin, D.P., and Rome, E. 1989. Acoustic census of limnetic fish in a glacially turbid lake. Proc. Inst. Acoustics, **11**: 238–247.

McArdle, J., and Bullock, A.M. 1987. Solar ultraviolet radiation as a causal factor of "summer syndrome" in cage-reared Atlantic salmon, *Salmo salar* L: a clinical and histopathological study. J. Fish Diseases, **10**: 255–264.

Salo, H.M., Aaltonen, T.M., Markkula, S.E., and Jokinen, E.I. 1998. Ultraviolet B irradiation modulates the immune system of fish (*Rutilus rutilus*, Cyprinidae). I. Phagocytes. Photochem. Photobiol. **67**: 433–437.

Sawada, J. 1993. An examination of differential survival in downstream migrating coho salmon smolts. M.Sc. thesis, Department of Zoology, The University of British Columbia, Vancouver, B.C.

Schindler, D.W., Curtis, P.J., Parker, B.R., and Stainton, M.P. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. Nature (London), **379**: 705–708.

Simpson, K., Diewert, R., Kadowaki, R., Cross, C., and Lehman, S. 1997. A 1996 update of assessment information for Strait of Georgia coho salmon stocks (including the Fraser River). Pacific Stock Assessment Review Committee, PSARC Working Paper S97.

Tarasick, D.W., Kerr, J.B., Wardle, D.I., Bellefleur, J.J., Bunka, S., and Davies, J. 1996. Trophospheric ozone trends at Canadian stations: 1980–1995. Proc. Quad. Ozone Symp., l'Aquila, Italy, Sept. 1996 (http://exp-studies.tor.ec.gc.ca/papers.htm).

Williamson, C.E., Metzgar, S.L., Lovera, P.A., and Moeller, R.E. 1997. Solar ultraviolet radiation and the spawning habitat of yellow perch, *Perca flavescens*. Ecol. Appl. **7**: 1017–1023.

Zagarese, H.E., and Williamson, C.E. 1994. Modeling the impacts of UV-B radiation on ecological interactions in freshwater and marine ecosystems. *In* Stratospheric ozone depletion/UV-B radiation in the biosphere. *Edited by* R.H. Biggs and M.E.B. Joyner. Springer-Verlag, Berlin. pp. 315–328.

© 1998 NRC Canada

Why restriction fragment length polymorphism analysis of mitochondrial DNA failed to resolve sardine (*Sardinops*) biogeography: insights from mitochondrial DNA cytochrome *b* sequences

W. Stewart Grant, A.-M. Clark, and Brian W. Bowen

Abstract: Restriction fragment length polymorphism (RFLP) and nucleotide sequence analysis of mitochondrial DNA (mtDNA) have generated conflicting hypotheses on the phylogeography of Indian–Pacific clupeid *Sardinops*. An RFLP analysis of the control region and adjoining segments indicates a phylogenetic affiliation between southern Africa – Australian and Japanese sardines whereas comparisons of an overlapping segment of the control region sequence indicate an affiliation between southern Africa – Australian and Chile–Californian sardines. An analysis of 258 bp of mtDNA cytochrome *b* in 74 individuals of *Sardinops* from South Africa, Australia, Chile, California, and Japan revealed 24 haplotypes, resulting in high levels of haplotypic (h) diversity (average h = 0.70), low levels of nucleotide (π) diversity (average π = 0.005), and a satisfactory level of divergence (d) for population resolution (d_{max} = 4.02%). Cluster and parsimony analyses of haplotypic divergences confirmed the existence of three lineages corresponding to southern Africa – Australia, Chile–California, and Japan but failed to confirm a biogeographic connection between Australia and Japan. These results support the model based on control region sequences and highlight potential pitfalls of RFLP analyses of highly polymorphic DNA sequences with numerous homoplaseous transitions. A comparaison of 220 bp of cytochrome *b* in samples of *Sardina* and *Sardinops* produced an average sequence divergence of 23.2% and supports an ancient divergence between *Sardina* and *Sardinops*. The three lineages of Indian–Pacific *Sardinops* may merit subspecies recognition, based on low but significant levels of mtDNA divergence between them and on evidence of separations between these groups on the order of 200 000 – 500 000 years.

Résumé : Le polymorphisme de taille des fragments de restriction et l'analyse des séquences nucléotidiques de l'ADN mitochondrial (ADNmt) ont généré des hypothèses contradictoires sur la phylogéographie des clupéidés du genre *Sardinops* de la région indo-Pacifique. Une analyse utilisant le polymorphisme de taille des fragments de restriction de la région de régulation et des segments voisins montre l'existence d'une filiation phylogénétique entre les sardines de l'Afrique du Sud et de l'Australie, d'une part, et les sardines du Japon, d'autre part, tandis que des comparaisons d'un segment chevauchant de la séquence de la région de régulation montre l'existence d'une filiation entre les sardines de l'Afrique du Sud et de l'Australie, d'une part, et les sardines du Chili et de Californie, d'autre part. L'analyse de 258 pb d'ADNmt du cytochrome *b* chez 74 *Sardinops* d'Afrique du Sud, d'Australie, du Chili, de Californie et du Japon a révélé l'existence de 24 haplotypes, chez lesquels on a observé une forte diversité haplotypique (h, h moyen = 0,70), une faible diversité nucléotidique (π, π moyen = 0,005) et un niveau satisfaisant de divergence pour la résolution des populations (d_{max} = 4,02%). Les analyses typologiques et de parcimonie des divergences haplotypiques ont confirmé l'existence de trois lignées correspondant aux régions suivantes : Afrique du Sud – Australie, Chili–Californie et Japon, mais elles n'ont pu confirmer l'existence d'un lien biogéographique entre l'Australie et le Japon. Ces résultats viennent appuyer le modèle fondé sur les séquences de la région de régulation et mettent en lumière les lacunes potentielles des analyses utilisant le polymorphisme de taille des fragments de restriction pour les séquences d'ADN hautement polymorphiques avec de nombreuses transitions homoplasiques. Une comparaison de 220 pb du cytochrome *b* dans des échantillons de *Sardina* et de *Sardinops* a donné une divergence de séquences moyenne de 23,2% et confirme la divergence établie dans le passé entre ces deux genres. L'existence des trois lignées de *Sardinops* dans la région des océans Indien et Pacifique pourrait justifier l'établissement de sous-espèces, d'après la divergence faible mais

Received July 15, 1997. Accepted January 6, 1998.
J14112

W.S. Grant.[1] Conservation Biology Division, Northwest Fisheries Science Center, 2725 Montlake Blvd. East, Seattle, WA 98112, U.S.A.
A.-M. Clark. Molecular Services Core, P.O. Box 110700, University of Florida, Gainesville, FL 32611, U.S.A.
B.W. Bowen. Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653-3071, U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: stew.grant@noaa.gov

© 1998 NRC Canada

significative de l'ADNmt entre elles et d'après les indices de séparations entre ces groupes, séparations remontant à 200 000 – 500 000 ans.

[Traduit par la Rédaction]

Introduction

Nonconcordance among molecular data sets is well known. Contrasting results may not be the product of incorrect interpretation or flawed data, but may reflect legitimate differences in four areas of analysis. First, nonconcordance can arise from the analysis of different classes of DNA. The results of allozyme studies, for example, do not always agree with mtDNA analysis (e.g., Burton 1994) or with nuclear DNA assays (Karl and Avise 1992; Palumbi and Baker 1994). Typically, these contrasting results are attributable to differences in selection pressures and the inheritance of distinct classes of genetic markers. For example, in species with male-biased dispersal, an analysis of maternally inherited mitochondrial DNA (mtDNA) lineages will yield results quite different from an analysis of biparentally inherited nuclear DNA lineages (Karl et al. 1992). A second source of disagreement can arise from the analysis of DNA sequences with different evolutionary rates such that patterns of divergence are recorded in some sequences but not in others (e.g., Chapman et al. 1994). A third source may arise from differences in laboratory methods. For example, indirect analyses of DNA sequence variability with restriction enzymes (restriction fragment length polymorphism (RFLP)) are incapable of distinguishing more frequent, and often homoplaseous, transitions from less frequent transversions whereas these subsitutions are readily distinguishable with direct DNA sequence comparisons. A fourth source of nonconcordance may be the use of different analytical approaches. Some clustering algorithms, for example, may be inappropriate for detecting particular patterns of divergence (Lessa 1990; Hillis et al. 1994).

Two recent studies of mtDNA sequence variability have resolved several aspects of the genetic relationships among the five regional forms of sardines (*Sardinops*, Hubbs 1929) in the Indian–Pacific Ocean (Fig. 1), but the studies reach conflicting conclusions on other aspects. In a direct comparison of 500-bp sequences in the control region of mtDNA, Bowen and Grant (1997) showed that *Sardinops* consists of three major groups, southern Africa – Australia, Chile–California, and Japan, with an average sequence divergence between the groups of $d = 3.8\%$. Their results also indicate that the regional populations are connected in a linear biogeographic array extending from southern Africa, through Australia, Chile, California, and Japan. In an analysis of sardine mtDNA sequence variability with RFLP analysis of polymerase chain reaction (PCR) products of the control region and adjacent segments, Okazaki et al. (1996) observed the same three major geographical groups, but concluded that southern Africa – Australia and Japan were more closely related to each other than were southern Africa – Australia and Chile–California. Contrary to Bowen and Grant (1997), Okazaki et al. (1996) suggested a biogeographic connection between the Northern and Southern hemispheres across the tropical western Pacific Ocean rather than across the tropical eastern Pacific.

A second controversy exists over the origins and age of Indian–Pacific *Sardinops*. One school maintains that ancestral populations of Indian–Pacific *Sardinops* and Atlantic–Mediterranean *Sardina* (Walbaum 1792) were isolated by the closure of the Tethys Sea about 18 million years ago (Svetovidov 1952; Parrish et al. 1989). This scenario is supported by a large allozyme divergence between *Sardina* and *Sardinops* (Grant and Leslie 1996). In contrast, Okazaki et al. (1996) postulated that *Sardinops* was derived from *Sardina* by the rise of the Isthmus of Panama about 3 million years ago.

A third constroversy involves the formal taxonomies of Indian–Pacific sardines, which are confounded by the lack of strong morphological differentiation among regional forms. Hubbs (1929) found few morphological differences among *Sardinops* populations in separate ocean basins, but nevertheless used Latin names to designate the various regional forms: *Sardinops ocellatus* (Pappe 1853) (southern Africa), *Sardinops neopilchardus* (Steindachner 1879) (Australia), *Sardinops sagax* (Jenyns 1842) (Chile–Peru), *Sardinops caeruleus* (Girard 1856) (Mexico–California), and *Sardinops melanostictus* (Temminck and Schlegel 1846) (Japan). Svetovidov (1952), however, maintained that all *Sardinops* belonged to a single species, *Sardinops sagax*, and designated regional forms as subspecies. Whitehead (1970) concurred with this treatment of *Sardinops* as five subspecies. Several authorities applied additional subspecific nomenclature to populations within regions (e.g., Lee 1961), but this has generally been rejected (Parrish et al. 1989) because of the lack of morphological and allozyme frequency differentiation between localities (Grant 1985; Hedgecock et al. 1989; Spanakis et al. 1989).

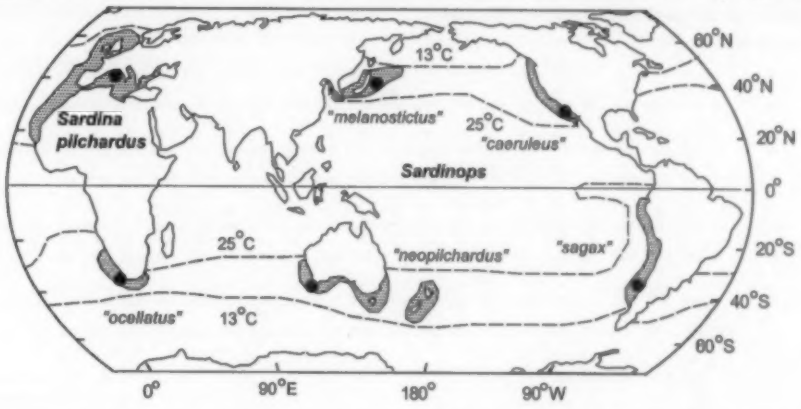
One goal of this study is to resolve the discrepancy between the biogeographic models for the five regional populations of *Sardinops* based on RFLP analysis and direct sequencing of the control region. The cytochrome *b* gene should provide an appropriate level of resolution to distinguish between the scenarios postulated by Okazaki et al. (1996) and Bowen and Grant (1997). A second goal is to test the conflicting temporal and biogeographic hypotheses of *Sardina–Sardinops* evolution using mtDNA cytochrome *b* sequence comparisons. Although molecular clocks are not precise, the amount of mtDNA cytochrome *b* divergence between these genera should provide an appropriate scale of temporal resolution to distinguish a mid-Pliocene (3 million years) from a Miocene (18 million years) divergence. Finally, we revisit the taxonomies of the regional forms of *Sardinops* in the light of the recent biochemical and molecular data.

Materials and methods

Skeletal muscle, heart, and liver tissues from *Sardina* in Europe and *Sardinops* in five regions in the Indian–Pacific Ocean (Table 1) were collected from 1983 to 1991 (Grant and Leslie 1996) and stored at –70°C until 1993 when heart and liver tissues were

© 1998 NRC Canada

Fig. 1. Geographic distributions (shaded areas) of sardines (*Sardina* and *Sardinops*) and localities of sample collections (solid circles).



placed in SED buffer (Amos and Hoelzel 1991) for shipment to the University of Florida, Gainesville.

Total DNA was isolated from about 200 mg of heart and liver tissue with the phenol – chloroform – isoamyl alcohol protocol of Hillis et al. (1996) and precipitated with cold 95% ethanol. Double-stranded amplifications of a partial cytochrome *b* gene were performed with PCR using biotinylated primers L14724, L14841, and H15149 (Irwin et al. 1991; Meyer 1994). An 18-base universal M13 sequence was added to the 5′ end of the primers to facilitate automated sequencing. Each PCR reaction included 5 μL of 10× buffer (200 mM Tris–HCl, pH 8.4, 500 mM KCl), 4.5 μL of 50 mM $MgCl_2$, 2 μL of 0.5 mM dNTP, 2 μL of each of 6.5 mM forward and reverse primers, 2 μL of template DNA in TE, 1 μL of *Taq* polymerase (Boehringer Mannheim), and 25.5 μL of water. PCR was initiated at 94°C for 3 min, followed by 34 cycles of 94°C for 1 min, 50°C for 1 min, and 72°C for 1 min and a final extension for 3 min at 72°C. Negative controls (template-free PCR reaction) were used to detect contamination, and samples from each locality were processed separately to avoid accidental mixing.

Double-stranded PCR products were purified by capture with streptavidin-coated magnetic beads (Dynabeads M280 streptavidin, Dynal, Sweden) and denatured with 0.2 M NaOH. The single-stranded template in solution was sequenced with fluorescently labeled M13 primers in an automated DNA sequencer (Applied Biosystems, model 373A) at the DNA Sequencing Core, University of Florida, Gainesville. Reverse sequences were generated for at least one representative of each haplotype and for unresolved forward sequences when necessary.

Comparisons of haplotypic frequencies between samples were made with a Monte Carlo χ^2 test and 1000 resamplings using REAP version 4.0 (McElroy et al. 1992). We compared South Africa and Australia and Chile and California at the lowest hierarchical level and three groups, South Africa – Australia, Chile–California, and Japan, at the highest level. REAP also produced unbiased estimates of haplotypic (h) and nucleotide (π) diversities (Nei 1987) using estimates of Kimura's two-parameter sequence divergence (d) between pairs of haplotypes, which were computed by MEGA (Kumar et al. 1993). The proportion of gene diversity within and between regions was estimated with Φ_{ST} (AMOVA, Excoffier et al. 1992), an analogue of F_{ST} applicable to DNA sequence data. The significance of each Φ_{ST} value was tested by comparison with a null distribution of random sampling from the global population and was based on 500 resampling trials with replacement.

A neighbor-joining tree (Saitou and Nei 1987) was generated from the matrix of d values, and 500 bootstrapped trees were used to evaluate levels of support for nodes in a majority-rule consensus tree. Clusters with bootstrap values above 50% were retained. PHYLIP programs (version 3.57, J. Felsenstein, Department of Genetics, University of Washington, Seattle, WA 98195) were used to produce maximum likelihood (DNAML) and parsimony (DNAPARS, DNAPENNY) trees. We also used multidimensional scaling (Kruskal 1964; PC-NTSYS, Exeter Software) with a minimum spanning tree to depict relationships among haplotypes. Finally, we superimposed a network of minimal mutational distances between haplotypes on a map of sample locations to infer phylogeographic patterns.

Table 1. Localities, date, sample size (n), number of haplotypes, and haplotypic (h) and nucleotide (π) diversities for samples of sardines (*Sardina* and *Sardinops*).

Locality (abbreviation)	Year	n	No. of haplotypes	h	π
Sardina					
Barcelona, Spain (EU)	1984	5	2	0.36	0.002
Sardinops					
Cape Town, South Africa (SA)	1991	15	5	0.62	0.004
Western Australia (AU)	1985	15	5	0.67	0.004
Iquique, Chile (CH)	1991	15	8	0.76	0.006
San Diego, California (CA)	1994	15	6	0.76	0.007
Hokkaido, Japan (JA)	1983	14	5	0.67	0.005
Average				0.70	0.005
Pooled				0.90	0.016

Results

Divergence between *Sardina* and *Sardinops*

Haplotype diversity (h) in *Sardina* (n = 5) was 0.36 and nucleotide diversity (π) was 0.002 (Table 1). Two haplotypes differing by a single transversion were observed in *Sardina*, based on a 220-bp fragment of cytochrome *b* (Table 2; Fig. 2). This fragment overlapped the sequences resolved in *Sardinops* beginning at position 39. A total of 26 transitions and eight transversions were observed between haplotypes in *Sardina* and those in *Sardinops*. The two genera differed by a minimum of d = 20.8% (between haplotype **B** in *Sar-*

© 1998 NRC Canada

Fig. 2. Mitochondrial cytochrome *b* nucleotide and amino acid sequences for 220 bp of haploytpe **A** in European sardines (*Sardina*) and 258 bp of haplotype **C** in Indian–Pacific sardines (*Sardinops*).

Table 2. Variable nucleotide positions of mtDNA cytochrome *b* and frequencies of haplotypes in sardines (*Sardina* and *Sardinops*).

| | Nucleotide position | | |

Fig. 3. Bootstrap neighbor-joining tree based on Kimura's two-parameter sequence divergence (*d*) between mtDNA cytochrome *b* haplotypes in sardines (*Sardina* and *Sardinops*). Numbers at nodes indicate bootstrap support for cluster to right of node.

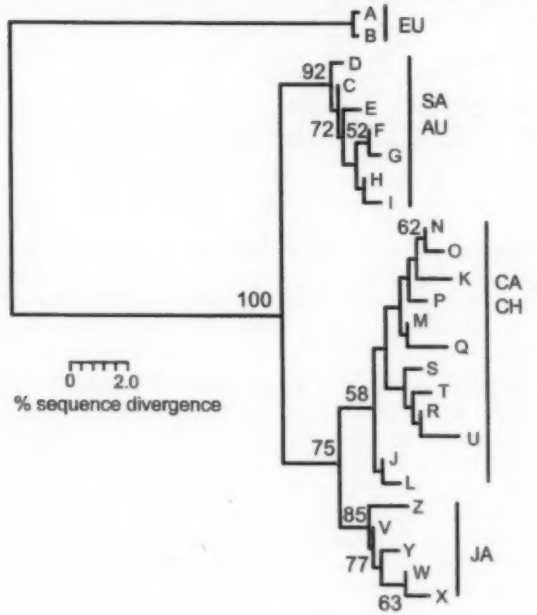
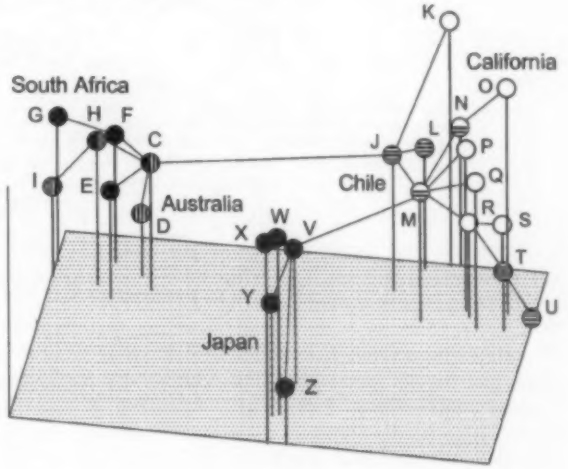


Fig. 4. Three-dimensional scaling of Kimura's two-parameter sequence divergence (*d*) between mtDNA cytochrome *b* haplotypes in sardines (*Sardinops*) with minimum spanning tree between haplotypes.



African sardines to 0.007 in Chilean sardines and averaged 0.005 (Table 1). Haplotype diversity in the pooled sample was 0.90, and nucleotide diversity was 0.016.

Differentiation between *Sardinops* populations

Pairwise calculations of Φ_{ST} were highly significant ($P < 0.001$) for all combinations of samples (range 0.690–0.799) except between South Africa and Australia ($\Phi_{ST} = 0.052$, $P = 0.46$) and between Chile and California ($\Phi_{ST} = 0.050$, $P = 0.10$). Monte Carlo χ^2 tests of haplotype frequencies were all significant except between South Africa and Australia ($P = 0.32$) and between California and Chile ($P = 0.07$). These pairs of samples were pooled, and a test of frequencies in three groups (South Africa – Australia, Chile–California, and Japan) was highly significant ($P < 0.0001$), as no haplotypes were shared between groups. An hierarchical analysis of molecular variance (AMOVA) indicated that 0.3% of the total haplotypic variability was due to differences between South Africa and Australia and between Chile and California, 75.8% was due to differences among the three groups, and 23.9% was contained within groups.

Phylogeography of *Sardinops* populations

Divergence (*d*) in the cytochrome *b* sequence between *Sardinops* haplotypes ranged from 0.39 to 4.02%. A neighbor-joining tree of these values resolved three groups corresponding to South Africa – Australia, Chile–California, and Japan, each with strong bootstrap support (Fig. 3). Chile–California and Japan cluster together relative to South Africa – Australia in the neighbor-joining tree based on cytochrome *b* sequences, a topology that is supported by maximum likelihood and parsimony analyses (not shown). In contrast, analyses of the control region sequences show an affiliation of Chile–California and South Africa – Australia relative to Japan. However, the two sequencies are concordant in indicating that Chile–California lies between the other two groups in all phylogenetic analyses and that the most divergent haplotypes are between South Africa – Australia and Japan. Multidimensional scaling and a minimum spanning tree illustrate this aspect of the data set (Fig. 4; see also fig. 3 in Bowen and Grant 1997). A parsimony network of nucleotide differences between haplotypes indicates that these three groups are related to each other in a linear array extending from South Africa, through Australia, Chile, and California, to Japan (Fig. 5).

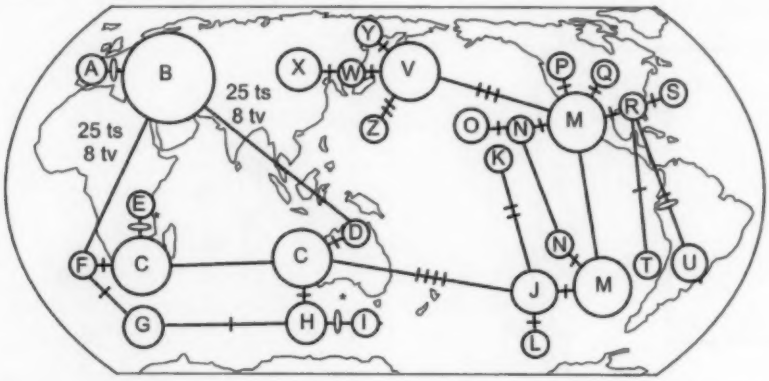
Discussion

Evolution of *Sardina* and *Sardinops*

One goal of this study was to estimate the timeframe for divergence between *Sardina* and *Sardinops* with mtDNA cytochrome *b* sequences to distinguish between a mid-Miocene separation (Grant and Leslie 1996), corresponding to the closure of the Tethys Sea by the collision of the African continental plate against Europe, and a mid-Pliocene separation (Okazaki et al. 1996), corresponding to the separation of the western Atlantic and eastern Pacific by the rise of the Isthmus of Panama. While molecular clocks are not precise, the fivefold difference in the age of the proposed separations (corresponding to 3 versus 18 million years) indicates that these geological events should readily be distinguishable by genetic distances between *Sardina* and *Sardinops*. In a study of allozyme variability, Grant and Leslie (1996) found that 23 of 34 protein-coding loci were fixed, or nearly fixed, for different alleles between these two genera and estimated Nei's $D = 1.0$. This level of divergence corresponds to 15–23 million years of separation based on a protein clock for marine fishes calibrated by genetic divergence between At-

© 1998 NRC Canada

Fig. 5. Parsimony network of nucleotide substitutions between mtDNA cytochrome *b* haplotypes in sardines (*Sardina* and *Sardinops*). Sizes of circles are proportional to frequencies of haplotypes. Lines across connections indicate transitions, and ovals indicate transversions. Asterisks indicate amino acid replacements.



lantic and Pacific sister species isolated by the Isthmus of Panama (Vawter et al. 1980) and by dispersal through the Bering Strait (Grant 1987). In the present study, the average cytochrome *b* sequence divergence of 23.2% between *Sardina* and *Sardinops* is at the upper end of (or beyond) the linear relationship between mtDNA divergence and time (Brown et al. 1979) and therefore may underestimate the amount of divergence between these taxa. Based on an mtDNA clock calibration of 2% per million years (Brown et al. 1979), this level of divergence represents at least 11 million years of isolation and is consistent with a vicariance model of Miocene separation.

Homoplasies and the phylogeography of *Sardinops*

Bowen and Grant (1997) have shown that dispersal between boundary current regions has been an important force in shaping genetic relationships among present-day *Sardinops* populations. While many zoogeographic conclusions of Okazaki et al. (1996) and Bowen and Grant (1997) are concordant, Okazaki et al. (1996) linked sardines in Japan and Australia in a phylogenetic analysis (bootstrap value 74%) whereas Bowen and Grant (1997) linked populations in Japan and California (bootstrap value 100%). The former connection would imply transplantation across the tropical Indo-Pacific, through a broad water mass above 27°C, a thermal regime that is lethal to sardines.

How can two surveys of the control region yield different tree topologies with relatively high bootstrap values? The difference between these conclusions bears careful scrutiny, as these comparisons can yield insights into some underappreciated limits of DNA sequence analyses. Okazaki et al. (1996) conducted RFLP analyses of a 2-kb fragment that included the control region and adjacent segments of cytochrome *b* and 12S rRNA. Ten restriction endonucleases (all with four-base recognition sites) revealed 78 haplotypes in 95 individuals. The total number of fragments assayed was not given in the paper, so it is uncertain how much sequence information was available. Bowen and Grant (1997) used direct sequence comparisons of a 500-bp segment of the control region, revealing 78 haplotypes in 81 individuals. Both studies observed the deepest divergences within *Sardinops* at about d = 7–8%, and both reported three clusters of haplotypes corresponding to South Africa – Australia, Chile–California, and Japan, each with strong bootstrap support.

To resolve this discrepancy, we compare a phylogeny of cytochrome *b* sequences with the results based on *d*-loop sequences and RFLP data. This coding sequence evolves at a slower pace than the control region in many vertebrates (see Brown et al. 1986) and hence should contain fewer homoplasies. The cytochrome *b* sequences differ from the control region sequences in indicating whether Chile–Californian sardines are more closely related to cohorts in Japan or South Africa – Australia. However, the two sequence-based analyses are concordant (and at odds with the RFLP data set) in indicating that Chile–California lies between the other two groups. Hence the cytochrome *b* data unequivocally support the phylogeographic pattern suggested by Bowen and Grant (1997), linking southern Africa – Australia to Chile–California to Japan.

In the control region sequence assessment, Bowen and Grant (1997) reported extensive homoplasy. For example, haplotypes in Australia and Japan, separated by seven transversions, contain transition homoplasies at more than 10 sites (Table 3). These transition homoplasies are a well-documented source of phylogenetic "noise" and are routinely eliminated from molecular systematic studies involving deeper evolutionary partitions. For *Sardinops* control region sequences, homoplasies are attributed to high haplotype diversity, presumably due to explosive population growth in the Pleistocene. Bowen and Grant (1997) addressed this problem by eliminating transitions from the data set for the phylogenetic analysis. The 22 observed transversions were sufficient to yield a phylogenetic signal in parsimony (CI = 1.0, RI = 1.0) and neighbor-joining analyses.

Recent authors have debated the role of RFLP analyses in an era of increasing access to DNA sequence data (Lamb et al. 1994; Walker et al. 1995; Abreu-Grobois et al. 1996). One underappreciated consideration is that RFLP analyses cannot distinguish between transitions and transversions, so that all nucleotide substitutions must be weighted equally in phylogenies. We suspect that herein lies the difference between trees based on RFLPs and direct sequences. In Table 3, we document that Japanese and Australian haplotypes

© 1998 NRC Canada

Table 3. Cases of suspected homoplasy in control region sequences of Australian and Japanese sardines that would affect RFLP analysis.

	Transversions							Transition homoplasies									
		1	1	2	2	2	3				1	1	1	2	2	2	4
	2	7	7	2	3	4	0	3	7	8	0	3	5	3	6	8	0
Sample	9	3	8	6	4	1	9	7	3	8	8	2	3	6	2	9	8
Japan	T	G	C	A	T	C	T	C	T/C	G/A	T	G/A	T	A	A	A/G	A
Australia	G	T	G	T	A	A	A	C/T	T	A	T/C	G	T/C	A/G	G/A	G/A	G/A

Note: The first seven columns indicate the nucleotide sites of transversion substitutions that are fixed between sample sites. The next 10 columns indicate the locations of transition homoplasies that occur in recognition sites for restriction enzymes used by Okazaki et al (1996). The first nucleotide listed is the more frequent nucleotide at that position. *Hha*I sites at 73, 236; *Mbo*I at 88; *Mse*I at 153, 262; *Msp*I at 37, 108, 408; *Taq*αI at 132, 289.

are characterized by at least 10 transition homoplasies at recognition sites for the restriction enzymes used by Okazaki et al. (1996). It is likely that a restriction enzyme analysis of these sequences would give a misleading result because homoplasies outnumber fixed transversion differences. In these circumstances, the RFLP analysis of control region sequences is suspect because it cannot distinguish transitions and transversions.

These explorations prompt a recognition of two seldom-considered characteristics of phylogenetic inference from DNA sequence data. First, direct sequencing offers a substantial advantage over RFLP data when saturation of nucleotide polymorphisms is known or suspected. In recent simulation studies, the methods that consistently performed best in recovering the correct molecular phylogeny all involved weighting for different positions and different types of mutations (Hillis et al. 1994). None of these conventional weighting schemes are applicable to RFLP data, and this can be a substantial handicap in resolving branches that may have diverged over relatively brief evolutionary intervals.

Second, the problem of multiple changes at a single site is not confined to deeper evolutionary genetic separations. The most parsimonious tree of Bowen and Grant (1997) based on control region sequences contains numerous homoplasies, yet the most divergent haplotypes in the tree are separated by a modest $d_{max} = 0.076$. In the cytochrome *b* sequences, suspected reversals also appear at sites 61 and 226 to produce the same character states in southern Africa – Australia and Japan. In both the control region and the cytochrome *b* data, identical transitions were observed in lineages which are well differentiated in all phylogenetic analyses. These homoplasies receive equal weight with transversions in the RFLP analysis, and this is certain to obscure the underlying phylogenetic signal.

Colonization history of *Sardinops* populations

Sardinops appears to have been isolated from *Sardina* for about 18 million years, yet the regional forms of *Sardinops* show a shallow genetic architecture that implies recent radiation. A time frame based on allozymes (Grant and Leslie 1996) indicates that the regional forms shared a common ancestor about 200 000 years ago. Divergences between the three major groups based on the analysis of control region sequences also point to a common ancestry about 300 000 – 500 000 years ago (Bowen and Grant 1997), or 200 000 – 260 000 years ago (Okazaki et al. 1996) using calibrations for rapidly evolving molecular clocks (Stewart and Baker 1994). Average sequence divergences for cytochrome *b* ranged from $d = 2.3\%$ between Chile–California and Japan to $d = 2.8\%$ between southern Africa – Australia and Japan. Since the rate of silent substitution in the third codon position of cytochrome *b* in higher vertebrates is about 10% per million years in early stages of divergence (Irwin et al. 1991), and since most of the substitutions observed in the present analysis of cytochrome *b* occurred in the third position, these divergences represent about 200 000 – 300 000 years since common ancestry. All of these estimates, as well as allozyme studies, point to a recent expansion of *Sardinops* around the Indian–Pacific rim.

Okazaki et al. (1996) used red-eye round herring (*Etrumeus teres*) as an outgroup for *Sardinops* comparisons and found that it was most closely related to Chile–Californian sardines. However, *Etrumeus* is only distantly related to sardines ($d > 15\%$ in the RFLP study), and in any case is not the sister taxon to *Sardinops*. *Sardina* is the closest taxon, but Bowen and Grant (1997) concluded that this genus was too distant in control region sequence analysis to provide a meaningful comparison. The more conservative evolutionary rate in cytochrome *b*, however, offers a potential comparison. Average sequence divergences for cytochrome *b* were lowest between southern Africa – Australia and *Sardina*; the common haplotype in *Sardina* was closest to two haplotypes in southern Africa – Australian sardines (33 mutational steps) and most distant from a haplotype in the California sample (39 steps). However, a difference of only six mutations after 10–20 millions years of isolation may not be meaningful for inferring an ancestral connection. Regional extinctions and recolonizations in *Sardinops*, combined with a relatively deep evolutionary separation from *Sardina*, preclude recovery of the early colonization history of *Sardinops* with available data.

Taxonomy of regional populations of *Sardinops*

Taxonomic issues for sardines have been contentious because morphologically similar forms of *Sardinops* occur in widely separated regions of the world. Hubbs (1929) first distinguished Atlantic and Indian–Pacific forms of sardines at the genus level and established species names for the five regional populations of *Sardinops*. However, Svetovidov (1952) concluded that morphological differentiation between the regional forms was insufficient to merit species assignments, a conclusion endorsed by Ahlstrom (1960). Both authors recognized the potential validity of subspecies assignments for at least some regional forms. This contro-

© 1998 NRC Canada

versy continued into the 1980s, when Whitehead (1985, p. 57) endorsed the five species designations based on the opinion that "the five populations are so widely separated geographically that any exchange of genetic material is either impossible or unlikely." After reviewing morphological studies and on the basis of limited allozyme data, Parrish et al. (1989) resurrected the possibility of a single panoceanic species. On the basis of RFLP data, Okazaki et al. (1996) endorsed species-level designations for the three primary evolutionary lineages: southern Africa – Australia, Chile–California, and Japan.

How do recent biochemical and molecular assays bear on this problem? All studies to date indicate a low level of divergence between the regional populations of *Sardinops*. Nei's allozyme genetic distances between the regional forms are less than 0.011 (Grant and Leslie 1996), a level of divergence typical between populations in the same species (Thorpe 1982). Conspecific populations of clupeiod fishes are usually characterized by allozyme genetic distances much less than 0.04 (*Clupea pallasi*, Grant and Utter 1984; *Clupea harengus*, Ryman et al. 1984; *Sardinella aurita*, Wilson and Alberdi 1991). The analyses of mtDNA (Okazaki et al. 1996; Bowen and Grant 1997; this study) also show population-level divergences between some regional forms. Sequence divergences for restriction enzyme surveys of whole mtDNA are usually less than 5% for intraspecific comparisons of marine fishes (*Clupea harengus*, Kornfield and Bogdanowicz 1987; *Alosa sapidissima*, Bentzen et al. 1989; *Brevoortia patronus*, Bowen and Avise 1990; *Sardinella aurita*, Tringali and Wilson 1993). Unlike the allozyme data, however, mtDNA data clearly show the existence of three monophyletic lineages, southern Africa – Australia, Chile–California, and Japan, that show reciprocal monophyly for both control region and cytochrome *b* haplotypes. Although Okazaki et al. (1996) suggested that these three groups be given species standing, the low level of divergence between them, overall morphological similarity, and their shallow evolutionary history argue against treating them as separate species. Nonetheless, mtDNA data indicate that the lineages have existed for hundreds of thousands of years. Based on these considerations, we recommend three subspecies designations: *Sardinops sagax ocellatus* (Pappe 1853) in southern Africa, Australia, and New Zealand, *Sardinops sagax sagax* (Jenyns 1842) in Chile, Peru, Ecuador, Mexico, the United States, and Canada, and *Sardinops sagax melanostictus* (Temminck and Schlegel 1846) in China, Korea, Japan, and Russia. Subspecies recognition of three regional groups is concordant with the recommendations of Svetovidov (1952) and Whitehead (1970), who did not have the benefit of molecular data, and is sufficient to reflect the evolutionary separations among regional forms.

Acknowledgements

This study greatly benefited from the contributions of R.W. Leslie, A. Garcia-Rodriguez, and A.L. Bass. J. Graves, T. Kobayashi, and J. Shaklee generously provided tissue samples. E. Almira and S. Shanker and the DNA Sequencing Core at the University of Florida provided technical support, and R. Chapman, P. Moran, and R. Waples offered insightful comments on a draft of the manuscript. The project was supported by the Biological Oceanography Program of the National Science Foundation, Washington, D.C., and by the Foundation for Research Development, Pretoria.

References

Abreu-Grobois, F.A., Bass, A.L., Dutton, P.H., and Encalada, S.E. 1996. PCR–RFLP analysis of sea turtle populations in the era of DNA sequencing. Is it still useful? *In* Proceedings of the International Symposium on Sea Turtle Conservation Genetics. *Edited by* B.W. Bowen and W.N. Witzell. NOAA Tech. Memo. NMFS-SEFSC-396. pp. 55–68.

Ahlstrom, E.H. 1960. Synopsis on the biology of the Pacific sardine (*Sardinops caerulea*). *In* Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Vol. 2. FAO, Rome. pp. 415–451.

Amos, B., and Hoelzel, A.R. 1991. Long-term preservation of whale skin for DNA analysis. Rep. Int. Whaling Comm. Spec. Issue, **13**: 99–103.

Bentzen, P., Leggett, W.C., and Brown, G.C.. 1989. Mitochondrial DNA polymorphism, population structure, and life history variation in American shad *Alosa sapidissima*. Can. J. Fish. Aquat. Sci. **46**: 1446–1454.

Bowen, B.W., and Avise, J.C. 1990. Genetic structure of Atlantic and Gulf of Mexico populations of sea bass, menhaden, and sturgeon: influence of zoogeographic factors and life history patterns. Mar. Biol. **107**: 371–381.

Bowen, B.W., and Grant, W.S. 1997. Phylogeography of the sardines (*Sardinops* spp.): assessing biogeographic models and population histories in temperature upwelling zones. Evolution, **51**: 1601–1610.

Brown, W.M., George, M., Jr., and Wilson, A.C. 1979. Rapid evolution of animal mitochondrial DNA. Proc. Natl. Acad. Sci. U.S.A. **76**: 1967–1971.

Brown, G.G., Gadaleta, G., Pepe, G., Saccone, C., and Sbisa, E. 1986. Structural conservation and variation in D-loop containing region of vertebrate mitochondrial DNA. J. Mol. Biol. **192**: 503–511.

Burton, R.S. 1994. Inferring the genetic structure of marine populations: a case study comparing allozyme and DNA sequence data. CalCOFI Rep. **35**: 52–60.

Chapman, R.L., Patton, J.C., and Eleby, B. 1994. Comparisons of mitochondrial DNA variation in four alosid species as revealed by the total genome, the NADH dehydrogenase I and cytochrome *b* regions. *In* Genetics and evolution of aquatic organisms. *Edited by* A.R. Beaumont. Chapman and Hall, London, U.K. pp. 249–263.

Excoffier, L., Smouse, P.E., and Quattro, J.M. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial restriction data. Genetics, **131**: 479–491.

Grant, W.S. 1985. Population genetics of the southern African pilchard, *Sardinops ocellata*, in the Benguela upwelling system. Int. Symp. Upw. W. Africa. Inst. Invest. Pesqui. Barcelona 1985 (1). pp. 551–562.

Grant, W.S. 1987. Genetic divergence between congeneric species of Atlantic and Pacific Ocean fishes. *In* Population genetics and fishery management. *Edited by* N. Ryman and F.M. Utter. University of Washington Press, Seattle, Wash. pp. 225–246.

Grant, W.S., and Leslie, R.W. 1996. Late Pleistocene dispersal of Indian–Pacific sardine populations in an ancient lineage of the genus *Sardinops*. Mar. Biol. **197**: 133–142.

© 1998 NRC Canada

Grant, W.S., and Utter, F.M. 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Can. J. Fish. Aquat. Sci. **41**: 856–864.

Hedgecock, D., Hutchinson, E.S., Li, G., Sly, F.L., and Nelson, K. 1989. Genetic and morphometric variation in the Pacific sardine, *Sardinops sagax caerulea*; comparisons and contrasts with historical data and with variability in the northern anchovy, *Engraulis mordax*. Fish. Bull. U.S. **87**: 653–671.

Hillis, D.M., Huelsenbeck, J.P., and Cunningham, C.W. 1994. Application and accuracy of molecular phylogenies. Science (Washington, D.C.), **264**: 671–677.

Hillis, D.M., Mable, B.K., Larson, A., Davis, S.K., and Zimmer, E.A. 1996. Nucleic acids IV: sequencing and cloning. *In* Molecular systematics. 2nd ed. *Edited by* D.M. Hillis, C. Moritz, and B.K. Mable. Sinauer Associates, Sunderland, Mass. Chap. 9, pp. 321–381.

Hubbs, C.L. 1929. The generic relationships and nomenclature of the California sardine. Proc. Calif. Acad. Sci. Ser. 4, **18**: 261–265.

Irwin, D.M., Kocher, T.D., and Wilson, A.C. 1991. Evolution of the cytochrome *b* gene of mammals. J. Mol. Evol. **32**: 128–144.

Karl, S.A., and Avise, J.C. 1992. Balancing selection at allozyme loci in oysters: implications from nuclear RFLPs. Science (Washington, D.C.), **256**: 100–102.

Karl, S.A., Bowen, B.W., and Avise, J.C. 1992. Global population genetic structure and male-mediated gene flow in the green turtle (*Chelonia mydas*): RFLP analysis of anonymous nuclear loci. Genetics, **131**: 163–173.

Kornfield, I., and Bogdanowicz, S.M. 1987. Differentiation of mitochondrial DNA in Atlantic herring, *Clupea harengus*. Fish. Bull. **85**: 561–568.

Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika, **29**: 1–27.

Kumar, S., Tamura, K., and Nei, M. 1993. MEGA: molecular evolutionary genetics analysis, version 1.01. Pennsylvania State University, University Park, Pa.

Lamb, T., Lydeard, C., Walker, R.B., and Gibbons, J.W. 1994. Molecular systematics of map turtles (*Graptemys*): a comparison of mitochondrial restriction site versus sequence data. Syst. Biol. **43**: 543–559.

Lee, J.Y. 1961. La sardine du golfe du Lion (*Sardina pilchardus*, *Sardina regan*). Rev. Trav. Inst. Pêches Marit. **25**: 419–511.

Lessa, E.P. 1990. Multidimensional analysis of geographic genetic structure. Syst. Zool. **39:** 242–252.

McElroy, D., Moran, P., Bermingham, E., and Kornfield, I. 1992. REAP: an integrated environment for the manipulation and phylogenetic analysis of restriction data. J. Hered. **83**: 157–158.

Meyer, A. 1994. Molecular phylogenetic studies of fish. *In* Genetics and evolution of aquatic organisms. *Edited by* A.R. Beaumont. Chapman and Hall, London, U.K. pp. 219–248.

Nei, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York.

Okazaki, T., Kobayashi, T., and Uozumi, Y. 1996. Genetic relationships of pilchards (genus: *Sardinops*) with anti-tropical distributions. Mar. Biol. **126**: 585–590.

Palumbi, S.R., and Baker, C.S. 1994. Contrasting population structure from nuclear intron sequences and mtDNA of humpback whales. Mol. Biol. Evol. **11**: 426–435.

Parrish, R.H., Serra, R., and Grant, W.S. 1989. The monotypic sardines *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure, and zoogeography. Can. J. Fish. Aquat. Sci. **46**: 2019–2036.

Ryman, N., Lagercrantz, U., Andersson, L., Chakraborty, R., and Rosenberg, R. 1984. Lack of correspondence between genetic and morphologic variability patterns in Atlantic herring (*Clupea harengus*). Heredity, **53**: 687–704.

Saitou, N., and Nei, M. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. **4**: 406–425.

Spanakis, E., Tsimenides, N., and Zouros, E. 1989. Genetic differences between populations of sardines, *Sardina pilchardus*, and anchovy, *Engraulis encrasicolus*, in the Aegean and the Ionian seas. J. Fish Biol. **35**: 417–437.

Stewart, D.T., and Baker, A.J. 1994. Patterns of sequence variation in the mitochondrial d-loop region of shrews. Mol. Biol. Evol. **11**: 9–21.

Svetovidov, A.N. 1952. Fishes: Clupeidae. Fauna U.S.S.R. (New Ser.), **48**. (Transl. Isr. Program Sci. Transl., Jerusalem.)

Thorpe, J.P. 1982. The molecular clock hypothesis: biochemical evolution, genetic differentiation and systematics. Annu. Rev. Ecol. Syst. **13**: 139–168.

Tringali, M.D., and Wilson, R.R., Jr. 1993. Differences in haplotype frequencies of mtDNA of the Spanish sardine *Sardinella aurita* between specimens from the eastern Gulf of Mexico and southern Brazil. Fish. Bull. U.S. **91**: 362–370.

Vawter, A.T., Rosenblatt, R., Gorman, G.C. 1980. Genetic divergence among fishes of the eastern Pacific and the Caribbean: support for the molecular clock. Evolution, **34**: 705–711.

Walker, D., Burke, V.J., Barak, I., and Avise, J.C. 1995. A comparison of mtDNA restriction site vs. control region sequences in phylogeographic assessment of the musk turtle (*Sternotherus minor*). Mol. Ecol. **4**: 365–373.

Whitehead, P.J.P. 1970. The clupeoid fishes described by Steindachner. Bull. Br. Mus. (Nat. Hist.) Zool. **20**: 1–46.

Whitehead, P.J.P. 1985. FAO species catalogue. Vol. 7. Clupeoid fishes of the world (Suborder Clupeoidei). Part 1. Chirocentridae, Clupeidae and Pristigasteridae. UN Dev. Prog., Rome.

Wilson, R.R., Jr., and Alberdi, P.D., Jr. 1991. An electrophoretic study of Spanish sardine suggests a single predominant species in the eastern Gulf of Mexico, *Sardinella aurita*. Can. J. Fish. Aquat. Sci. **48**: 792–798.

© 1998 NRC Canada

Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence

D.P. Swain, G.A. Chouinard, R. Morin, and K.F. Drinkwater

Abstract: We compared habitat associations of southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) between the summer feeding season on the Magdalen Shallows and the overwintering period in the Cabot Strait. Data were from bottom trawl surveys conducted in September 1993, 1994, and 1995 and January 1994, 1995, and 1996. Both species occupied much deeper, warmer water in winter than in summer. The effect of cod age on temperature distribution reversed between the two seasons, with younger cod occupying warmer water than older cod in summer and colder water in winter. Selection of both depth and temperature by cod tended to be more significant in September than in January. The reduced statistical significance of habitat selection by cod in winter was associated with a more aggregated distribution in this season. The contrast between seasons in habitat associations was particularly strong for plaice. The median habitats occupied by plaice were 58–67 m and –0.1 to 0.3°C in September and 374–426 m and 5.2–5.4°C in January. Habitat selection by plaice was significant in both seasons, but significance tended to be greater in January. Degree of aggregation in plaice distribution was similar between the two seasons. Female plaice occupied significantly warmer water than males in September but not in January. The ecological and practical implications of this striking seasonal variation in habitat associations are discussed.

Résumé : Nous avons comparé les associations d'habitat de la morue franche (*Gadus morhua*) et de la plie canadienne (*Hippoglossoides platessoides*) dans le sud du golfe du Saint-Laurent entre la saison d'alimentation estivale sur le plateau Madelinien et la période d'hivernage dans le détroit de Cabot. Les données utilisées à cette fin proviennent de relevés au chalut de fond effectués en septembre 1993, 1994 et 1995 et en janvier 1994, 1995 et 1996. Les deux espèces fréquentaient en hiver des eaux beaucoup plus profondes et plus chaudes qu'en été. Chez la morue, l'effet de l'âge sur la répartition en fonction de la température s'inversait d'une saison à l'autre, les individus plus jeunes occupant des eaux plus chaudes que les poissons plus âgés en été, et des eaux plus froides en hiver. Chez cette espèce, la sélection de l'habitat en fonction de la température et de la profondeur était dans l'ensemble statistiquement plus prononcée en septembre qu'en janvier. Le seuil de signification plus faible associé à la sélection de l'habitat par la morue en hiver s'accompagnait d'une distribution plus agrégative durant cette saison. Le contraste entre les associations avec l'habitat observées en septembre et en janvier était particulièrement prononcé chez la plie canadienne. Les habitats médians occupés par cette espèce étaient caractérisés par une profondeur de 58 à 67 m et une température de –0,1 à 0,3°C en septembre et une profondeur de 374 à 426 m et une température de 5,2 à 5,4°C en janvier. La sélection de l'habitat par la plie était significative au cours des deux saisons, mais de façon générale plus prononcée en janvier. Le degré d'agrégation de la distribution de la plie était similaire au cours des deux saisons. Les femelles fréquentaient des eaux significativement plus chaudes que les mâles en septembre, mais pas en janvier. Les implications écologiques et pratiques de cette variation saisonnière spectaculaire des associations avec l'habitat sont examinées.

[Traduit par la Rédaction]

Received October 27, 1997. Accepted July 22, 1998.
J14266

D.P. Swain,[1] G.A. Chouinard, and R. Morin. Department of Fisheries and Oceans, Gulf Fisheries Centre, P.O. Box 5030, Moncton, NB E1C 9B6, Canada.
K.F. Drinkwater. Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, NS B2Y 4A2, Canada.

[1]Author to whom all correspondence should be addressed.
e-mail: swaind@mar.dfo-mpo.gc.ca

Introduction

Fish species and their assemblages are generally associated with particular ranges of physical environmental conditions. At large scales in the marine environment, the species composition of groundfish assemblages is often closely related to gradients of depth and temperature (e.g., Mahon and Smith 1989). Temperature is a key environmental factor for fishes (Fry 1971), controlling the rates of physiological processes and affecting many components of fitness (e.g., growth rate). The importance of depth per se is less obvious

© 1998 NRC Canada

and may be related to correlations with other important habitat variables like prey distribution, productivity, and sediment type. Identification of the habitat associations of marine fishes has become a recent focus of fisheries research (e.g., Nakken and Raknes 1987; Page et al. 1994; Perry and Smith 1994; Swain and Kramer 1995). Knowledge of habitat associations may provide explanations for changes in fish distributions (e.g., Rose et al. 1994; Swain and Kramer 1995) and for variation in catchability to fishing gear (Smith and Page 1996) and may lead to improved survey estimates of fish abundance (Smith et al. 1991).

Despite the current interest in identifying habitat associations of marine fishes, there have been few studies examining seasonal variation in these associations (Murawski and Finn 1988; Morgan and Brodie 1991; Perry and Smith 1994). Clark and Green (1991) reported pronounced seasonal variation in the preferred temperatures of juvenile Atlantic cod (*Gadus morhua*) in the laboratory. Perry and Smith (1994) provided a rare example of replicated quantitative comparisons of habitat associations between seasons for four groundfish species. They classified two species as "temperature-keepers," showing little variation in temperature associations between seasons, and one species as a "depth-keeper," maintaining similar depth distributions between seasons. In this study, we describe seasonal variation in habitat associations of Atlantic cod and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence. We compare habitat associations of cod and plaice, the dominant groundfish species in the southern Gulf, between their summer – early fall feeding grounds on the Magdalen Shallows and their overwintering grounds in the Cabot Strait and Sydney Bight.

Many fishes exhibit ontogenetic shifts in habitat use (Werner and Gilliam 1984). These shifts are attributed to size-dependent changes in predation risk and foraging abilities and are important determinants of inter- and intraspecific interactions. Coutant (1987) has suggested that temperature is an important cue used by fishes to partition habitats among species and life history stages. Several studies have identified ontogenetic shifts in temperature associations of cod, but the direction of these shifts has differed among studies. The temperatures occupied by cod decreased with age in the southern Gulf of St. Lawrence (Swain and Kramer 1995) and on the Scotian Shelf (Sinclair 1992) but increased with age in the Barents Sea (Nakken and Raknes 1987; Ottersen et al. 1998) and off Labrador (Rose et al. 1994). This inconsistency could indicate fundamental differences among populations of a single species in the effect of ontogeny on temperature preference. However, the studies reporting older cod in colder water were conducted in summer and early fall whereas those reporting the opposite pattern were conducted in late fall and winter. This raises the possibility that this inconsistency reflects a seasonal difference rather than a population difference. We compare ontogenetic shifts in habitat associations among seasons for the same cod population.

Temperature preference is predicted to depend on food ration (e.g., Crowder and Magnuson 1983). A general agreement has been noted between the preferred temperature of fishes and the optimum temperature for performance of physiological processes like growth (Coutant 1987, and references therein). However, the optimum temperature for growth depends on food ration, decreasing as ration decreases (Brett et al. 1969; Woiwode and Adelman 1991). Thus, preferred temperature is also predicted to decrease as ration decreases. In laboratory tests, fish receiving reduced rations do tend to occupy colder temperatures, although the change in temperature distribution is generally small and less than that required to maximize growth (e.g., Mac 1985; Wildhaber and Crowder 1990; Morgan 1993). Field data also provide some support for this prediction. During the feeding season in the southern Gulf of St. Lawrence, cod tend to occupy colder water in years of high abundance (when food ration may be reduced due to increased competition) (Swain and Kramer 1995). Foraging rate often varies seasonally in fishes. Little feeding appears to occur during the overwintering period in some Northwest Atlantic groundfish populations including southern Gulf cod and plaice (e.g., Powles 1965; Schwalme and Chouinard 1999). We predicted, based on these bioenergetic considerations, that colder temperatures should be occupied during the overwintering period to reduce metabolic costs while fasting. A third objective of this study is to test this prediction.

Swain (1997) reported that female plaice tend to occupy warmer water than males in September during the feeding season in the southern Gulf of St. Lawrence. Female plaice have a faster growth rate than males in the southern Gulf. The hypothesis proposed to explain the difference in temperature distribution between the sexes was that the optimum temperature for growth is higher in females due to a higher foraging rate (and thus, food ration) in females. Finally, we test the prediction that there should be no difference in temperature distribution between the sexes in winter when little feeding occurs.

Material and methods

Study areas and populations

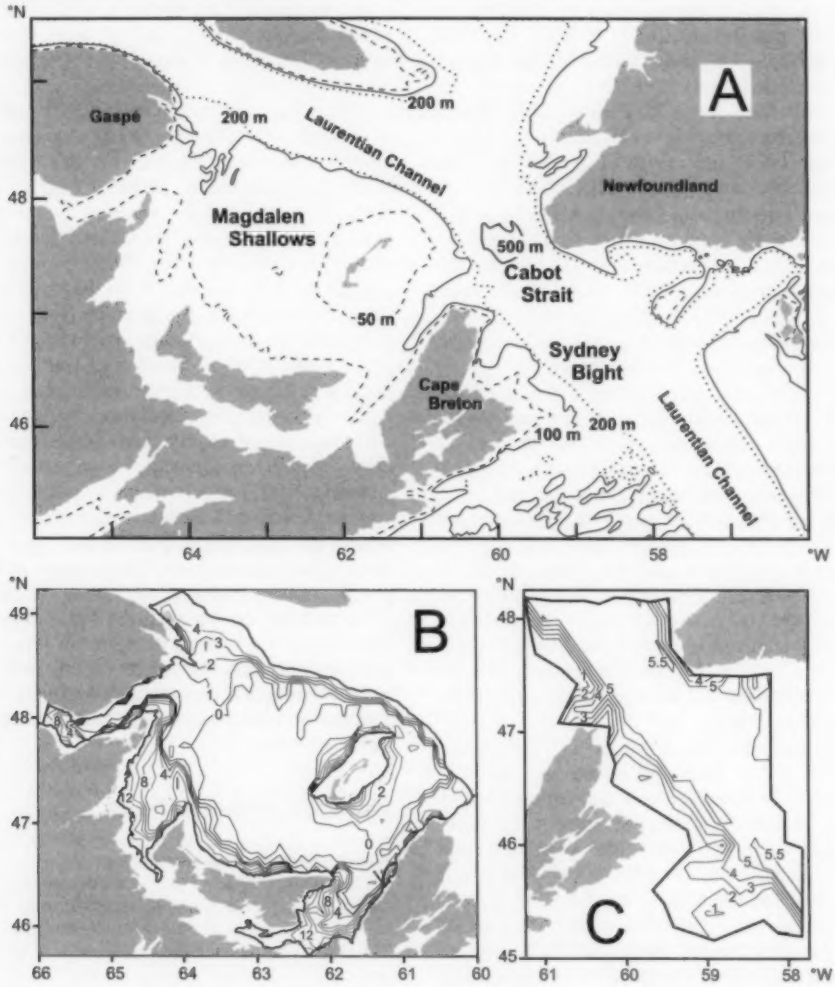
The southern Gulf of St. Lawrence consists of a shallow shelf, the Magdalen Shallows, with depths mostly less than 100 m, bordered on the north by a 500-m trench, the Laurentian Channel (Fig. 1A). Three water layers are present in the southern Gulf in summer and autumn: a warm surface layer, a cold intermediate layer (at depths of about 30–100 m), and a warm deep layer (Gilbert and Pettigrew 1997). The cold intermediate layer covers the bottom over much of the Magdalen Shallows, with bottom temperature increasing shoreward as depth decreases and toward the Laurentian Channel as depth increases (Fig. 1B).

The Cabot Strait area is dominated by the Laurentian Channel, with depths less than 100 m restricted to nearshore areas off the coasts of Cape Breton and Newfoundland and to offshore banks to the east (Fig. 1A). Two water layers are present in winter in this area: a cold surface layer and a warm deep layer. Bottom temperatures are relatively cold in the shallow inshore areas and on the banks and increase with depth along the slope of the Laurentian Channel (Fig. 1C).

Cod and plaice migrate onto the Magdalen Shallows in spring (April–May), spawn, and then disperse throughout the Shallows for a feeding period lasting from May to October (Jean 1964; Powles 1965). Examples of cod and plaice distributions on the Shallows during this feeding season are shown in Fig. 2. In November and early December, both species migrate off the Shallows to overwintering grounds in the Laurentian Channel. For cod, these overwintering grounds are located in the Cabot Strait and Sydney

© 1998 NRC Canada

Fig. 1. (A) Bathymetry in the southern Gulf of St. Lawrence and Cabot Strait areas. (B) Bottom temperature in the southern Gulf in September 1994. Contour interval is 1°C below 4°C and 2°C above 4°C. (C) Bottom temperature in the Cabot Strait in January 1995. Contour interval is 1°C below 5°C and 0.5°C above 5°C.



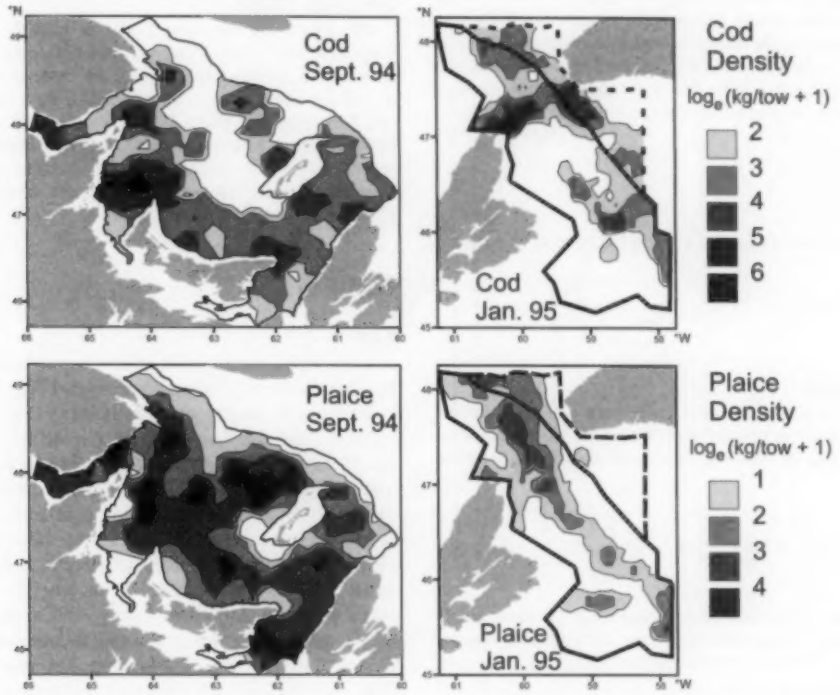
Bight areas (Halliday 1974). Cod from the northern Gulf also migrate into this area in winter, but this stock occupies the northern slope of the Laurentian Channel whereas the southern Gulf stock occupies the southern slope (e.g., Martin and Jean 1964; Gascon et al. 1990). Southern Gulf cod may mix with resident cod in the Sidney Bight (Northwest Atlantic Fisheries Organisation (NAFO) division 4Vn) area in winter (e.g., Martin and Jean 1964). However, the southern Gulf stock is much larger than the resident 4Vn stock, so the majority of cod in this area in winter are believed to be of southern Gulf origin (Halliday 1974; Mohn et al. 1997). Plaice also use the Cabot Strait and Sydney Bight areas over winter, although their overwintering grounds may extend throughout much of the Laurentian Channel, from this area to areas north of the Magdalen Islands and east of the Gaspé (Powles 1965; R. Morin, unpublished analyses). Examples of cod and plaice distributions in the Cabot Strait area in January are shown in Fig. 2.

Data sources

Data are from bottom trawl surveys conducted in the southern Gulf of St. Lawrence (NAFO division 4T) in September 1993, 1994, and 1995 by the research vessel *Alfred Needler* and in the Cabot Strait area in January 1994, 1995, and 1996 by the *Alfred Needler* or *Wilfred Templeman* (1996). The September surveys and the 1994 January survey followed a stratified random design. Stations for the 1995 and 1996 January surveys were allocated following a regular 12 × 12 nautical mile grid (with an additional station allocated midway between the regular grid points in areas along the 200-m contour where cod concentrations were expected). The 1994 January survey was restricted to areas on the south side of the Laurentian Channel (in NAFO divisions 4T and 4Vn) whereas the 1995 and 1996 January surveys also covered areas on the north side of the Channel (in divisions 4R and 3Pn). However, analyses reported here are restricted to the 4T–4Vn area on the south side of the Channel (Fig. 2), where most southern Gulf cod overwinter (e.g., Martin and Jean 1964). Stations in the 4R and 3Pn areas were omitted because most cod in these areas are from the northern Gulf population (Gascon et al. 1990). We excluded northern Gulf cod from the January analyses because habitat associations may differ between the northern and southern Gulf populations (Caston-

© 1998 NRC Canada

Fig. 2. Distributions of cod and plaice in the southern Gulf of St. Lawrence in September 1994 and in the Cabot Strait in January 1995. Interpolation is by ordinary kriging of log-transformed data. Solid lines enclose survey areas used in these analyses; broken lines enclose areas surveyed in January but not included in the analyses.



guay et al. 1999) and only the southern Gulf population is included in the September analyses. Cod catches in the 4Vn area in January are also expected to include some contribution by the resident 4Vn stock and possibly other stocks. The 1994 and 1995 September surveys covered the 4Vn area as well as 4T. Most of the analyses reported here are restricted to the 4T portions of these surveys (strata 415–439). For September 1994, results for cod are compared between 4T alone and 4T+4Vn (strata 415–442; see fig. 1 in Halliday and Koeller 1981) to illustrate the effect of including the 4Vn stock (as in the January surveys). In the 1995 September survey, a single tow (set 127) caught an exceptionally large number of small cod. This tow was considered an outlier (see Sinclair et al. 1996 for details) and omitted from analyses for cod.

Surveys conducted by the *Alfred Needler* used a Western IIA bottom trawl whereas that conducted by the *Wilfred Templeman* used a Campelen 1800 trawl. Target fishing procedures were a 30-min tow at 3.5 kn by the *Alfred Needler* or a 15-min tow at 3 kn by the *Wilfred Templeman*. All catches were adjusted to a standard tow of 1.75 nautical miles for the *Alfred Needler* surveys or 0.75 nautical mile for the *Wilfred Templeman* survey. Cod otoliths were removed from a length-stratified subsample of each catch for age determination, and the cod catch-at-age was determined by applying a survey-wide age–length key to the length distribution of each catch. Sex composition of plaice catches was determined by examining each fish in small catches or a random sample of at least 200 individuals in large catches.

Near-bottom temperatures were obtained from CTD casts made after each trawl tow. CTD casts were not made or did not closely approach the tow depth for 30–45% of the tows in the January surveys. In these cases, temperature at the tow depth was optimally estimated (Bretherton et al. 1976) from temperature data at neighbouring sites and at shallower depths at the target sites. The average of the depths at the start and the end of a tow was taken as the tow depth.

Habitat associations

We examined associations of cod and plaice with depth and temperature. Following Perry and Smith (1994), we used cumulative distribution functions (CDFs) to characterize habitat associations. We characterized the available habitat in each survey using the following CDF (percent):

$$(1)\qquad f(t) = 100\sum_{i=1}^{n} w_i I \text{ where } I = \begin{cases} 1, \text{ if } x_i \le t \\ 0, \text{ otherwise} \end{cases}$$

where t is a level of temperature or depth, w_i is the proportion of the survey area associated with tow i, n is the number of trawl tows in the survey, and x_i is the hydrographic measurement (i.e., bottom temperature or depth) for tow i. For the stratified surveys, w_i is the proportion of the survey area in the stratum fished by tow i divided by the number of tows made in that stratum. For the surveys using a regular grid design, w_i was taken as $v_i/\Sigma v_i$ where v_i was 1 for all tows except those in regions with extra stations added to the grid (where v_i was 0.5 for the extra station and 0.75 for each of its two neighbours).

We similarly calculated the CDF for fish catch in relation to temperature or depth for each year:

$$(2)\qquad g(t) = 100\sum_{i=1}^{n} w_i \frac{y_i}{\bar{Y}} I \text{ where } I = \begin{cases} 1, \text{ if } x_i \le t \\ 0, \text{ otherwise} \end{cases}$$

where y_i is the number of fish caught in tow i and $\bar{Y}$ is the mean catch per tow (calculated using the weights w_i). We calculated $g(t)$

© 1998 NRC Canada

separately for each age-class from 2 to 7+ years for cod and for each sex for plaice. A January 1 birthday is normally used when assigning ages to 4T cod. However, to facilitate comparisons between seasons, ages used for cod caught in January are those for the preceding September. Using $f(t)$ and $g(t)$, we calculated the median temperatures and depths available and those occupied by cod and plaice, as well as the 10th and 90th percentiles of available and occupied temperatures and depths. We also calculated the average temperature and depth available each year:

$$(3) \qquad H_{AV} = \sum_{i=1}^{n} w_i x_i$$

and the average temperature or depth occupied by cod or plaice:

$$(4) \qquad F_{AV} = \sum_{i=1}^{n} w_i \frac{y_i}{\bar{Y}} x_i.$$

Randomization tests

Following Perry and Smith (1994), we used a Kolmogorov–Smirnov type of statistic to test the significance of habitat associations. The test statistic D was the maximum difference between $g(t)$ and $f(t)$:

$$(5) \qquad \max_{\forall t} \left| g(t) - f(t) \right| = \max_{\forall t} \left| \sum_i w_i \left(\frac{y_i - \bar{Y}}{\bar{Y}} \right) I(x_i) \right|.$$

Statistical significance was assessed by comparing the observed D with the distribution of values obtained from 2999 random permutations of the data (3000 permutations including the observed data). Each permutation was conducted by randomly pairing the catch weights $w_i[(y_i - \bar{Y})/\bar{Y}]$ and the environmental factor x_i by sampling with replacement the observed x_i with probability w_i.

We also used randomization tests to assess the differences in temperature distribution between male and female plaice. For each measure of temperature distribution, the test statistic was the absolute value of the difference between the values for females and males (e.g., the median temperature occupied by females minus the median for males). The randomization procedure, conducted 2999 times, involved randomly redistributing plaice catches between males and females. For each tow, one of the observed catches was randomly assigned to males and the other to females. This procedure preserves the observed distribution of plaice with respect to temperature, assuming that differences between the catches of males and females at a particular temperature (i.e., in a particular tow) are due to chance alone.

Measures of aggregation

The power of these randomization tests depends on the degree of aggregation in fish distribution. A given value of D will be less significant according to randomization tests if fish are highly aggregated than if they are more evenly distributed. This occurs because large jumps in the catch-weighted CDF exist even with random pairings of catch and environmental variables when most of the fish abundance is found in few large catches. In these cases, the association between fish and particular levels of environmental variables could reflect either habitat selection or chance. We used Lorenz curves (Dagum 1985) to compare the degree of aggregation between September and January. To construct these curves, we calculated the estimated percentage of the population associated with each tow i ($N_i = 100 w_i y_i / \bar{Y}$) and the percentage of the area associated with each tow ($A_i = 100 w_i$). We sorted the tows by N_i and plotted cumulative percent area along the abscissa and cumulative percent abundance along the ordinate. The resulting Lorenz curve becomes more concave as fish distribution becomes more aggregated or concentrated.

Bivariate CDFs

We calculated bivariate CDFs to identify the habitat variable (depth or temperature) that was most strongly associated with fish distribution. In this case, f and g are three-dimensional surfaces in which the cumulative frequency forms the vertical axis (see eqs. 4 and 5 in Perry and Smith 1994). We compared the coordinates of D between univariate and bivariate CDFs. Perry and Smith (1994) reasoned that the variable with the strongest association with fish distribution was that whose coordinate changed the least going from univariate to bivariate tests.

Results

Cod

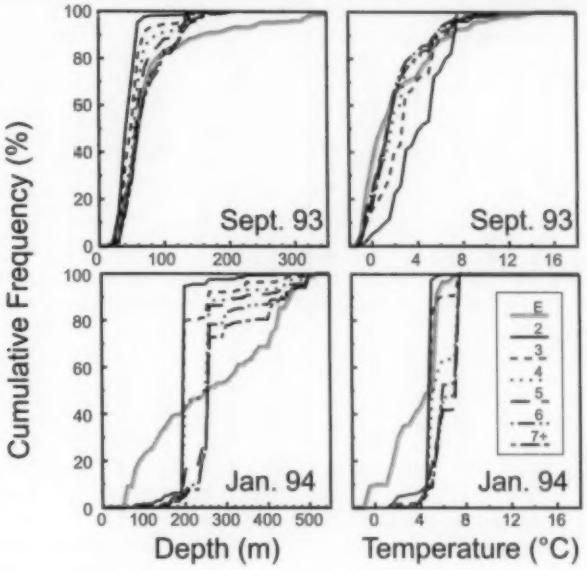
Cod depth distribution was similar among years but differed dramatically between seasons (Figs. 3 and 4). Cod occupied much deeper water in January than in September. For example, the median depths occupied by cod (age-2+) were 46–51 m in September and 195–244 m in January (Fig. 4). To a large extent, this difference between September and January in cod depth distribution reflects the difference between the Magdalen Shallows and the Cabot Strait area in available habitat. The median depth available on the Magdalen Shallows was about 60 m whereas that in the Cabot Strait area was 246–306 m (Fig. 4). On the other hand, relatively shallow depths in the 60–180 m range were available in the area surveyed in January but were avoided by cod (Fig. 3). This is reflected in the lower limits to cod depth distribution (Fig. 4). The 10th percentile of depth distribution in January was 72–86 m for the available habitat compared with 155–194 m for the cod-occupied (age-2+) habitat. The depths surveyed in the two seasons overlapped broadly, but the depths occupied by cod did not (Fig. 4). In all cases, the 90th percentile of cod depth distribution in September was much shallower than the 10th precentile of cod depth distribution in January (Fig. 4).

Younger cod tended to occupy shallower depths in both seasons (Figs. 3 and 4). For example, the average depth occupied by cod varied from 40–45 m for age-2 to 65–72 m for age-7+ in September and from 190–225 m for age-2 to 290–350 m for age-7+ in January.

Cod were significantly associated with depth in more cases in September than in January and for younger cod than for older cod (Table 1). The association with depth was significant for all ages of cod in September 1994, but only for younger cod in September 1993 (age-2 to age-4) and 1995 (age-2 to age-5). Cod associations with depth were not statistically significant in most cases in January. However, the nonsignificant values of D in January were as great or greater than the significant values in September (Table 1). The lack of significance in January reflects the high degree of aggregation by cod in January (Fig. 5). The consistent occurrence of cod aggregations in the same depths zones in each year (i.e., 150–200 m for age-2 and age-3 and greater than 200 m for older cod, e.g., Fig. 3) suggests that cod are not randomly distributed with respect to depth in January despite the low statistical significance of cod depth associations in winter.

© 1998 NRC Canada

Fig. 3. Cumulative distributions of cod catch in relation to depth and temperature for the 1993 September survey of the southern Gulf of St. Lawrence and the 1994 January survey of the Cabot Strait area. Distributions are shown for the habitats occupied by each age of cod from 2 to 7+ years and for the available habitat (*E*). January ages are those in the preceding September.



Cod temperature distributions were also similar among years but differed markedly between seasons (Figs. 3 and 4). Cod occupied much warmer water in January than in September. The median temperatures occupied by cod (age-2+) were 1.0–1.7°C in September and 4.9–5.3°C in January (Fig. 4). Cod were distributed much more narrowly with respect to temperature in January than in September. The difference in temperature distribution between seasons was most dramatic for older cod. In September, 75–85% of cod older than 4 years occurred at temperatures below 4°C whereas less than 5% of these older cod occurred at temperatures below 4°C in January. In September, young cod occupied warmer water than older cod. In January, the effect of age on temperature distribution was reversed, with younger cod occupying colder water than older cod. This reversal in ontogenetic effects on cod temperature distribution reflected wider seasonal variation in the temperatures occupied by older cod compared with younger cod. The average temperatures occupied by age-2 cod differed by less than 0.2°C between September and January whereas those occupied by age-5 cod differed by more than 3.5°C (Fig. 4).

The association of cod with temperature tended to be most significant for the younger ages in September and for the older ages in January (Table 1). In both cases, cod were associated with warm water relative to that available. As was the case for depth, the association with temperature was more often significant in September than in January. Again, this reflected the more aggregated distribution of cod in January, since *D* values for January were generally greater than those for September (Table 1). For older cod, differences between available and occupied temperatures do not appear to be substantial in September compared with those in January (Fig. 3). However, associations of these older cod with temperature are statistically significant as often in September as they are in January (Table 1).

Cod temperature distribution in September 1994 was similar including or excluding the 4Vn area (Fig. 6). The difference in cod habitat associations between the September and January surveys is clearly not simply a reflection of the mixture of southern Gulf cod with resident 4Vn cod in January.

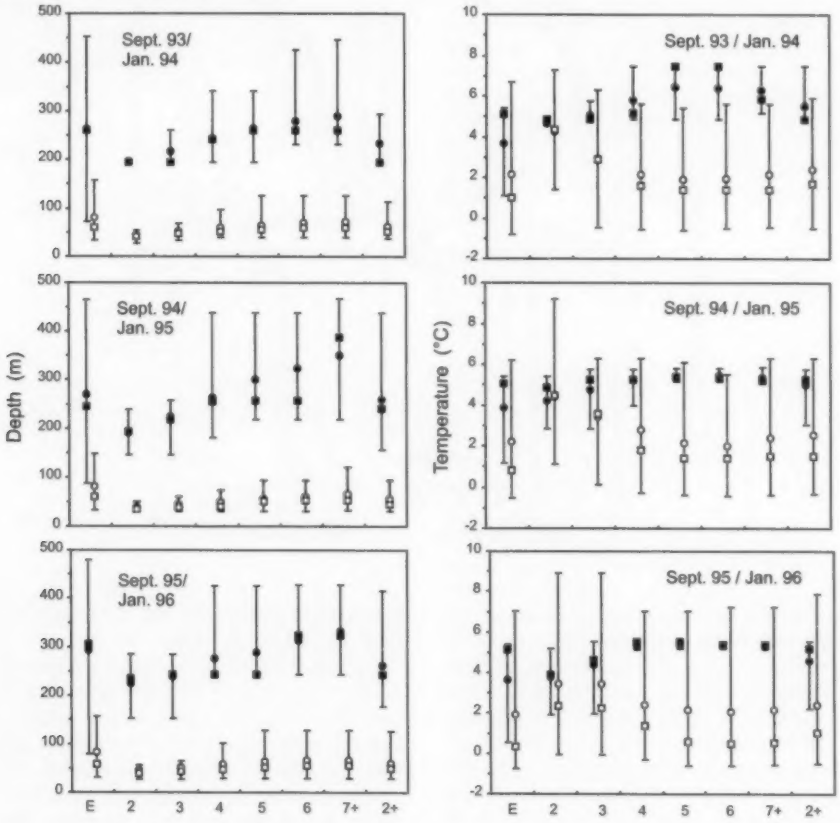
Cod habitat associations were significant equally often for depth and temperature in September. However, except for the oldest age group, the strength of these associations tended to be somewhat stronger for depth than for temperature (Table 1). For age-2 to age-5, the coordinate of *D* changed between univariate and bivariate tests for temperature but not for depth. The reverse occurred for age-7+ cod, suggesting a stronger association with temperature than with depth in September for the oldest age group of cod. In January, cod habitat associations were significant more often with temperature than with depth. Coordinates of *D* changed little between univariate and bivariate tests for temperature in January but changed greatly for depth in tests at the older ages (Table 1). Thus, cod appear to be more strongly associated with temperature than with depth in January, particularly for the older ages.

Plaice

Like cod, plaice occupied much deeper water in January than in September (Figs. 7 and 8). Median depths occupied by plaice were 58–67 m in September and 374–426 m in January, even deeper than the depths occupied by cod in January. There was little overlap between seasons in the depths occupied by plaice. In all cases, the 10th percentile of plaice depth distribution in January was deeper than the 90th percentile of their depth distribution in September. Depth

© 1998 NRC Canada

Fig 4. Summary statistics for cod depth and temperature distributions by age (2–7+ and 2+ years) in September in the southern Gulf of St. Lawrence (open symbols) and in January in the Cabot Strait area (solid symbols). Squares show the median; circles show the average. Lines extend from the 10th to the 90th percentile. January ages are those in the preceding September. *E* gives statistics for the depths and temperatures available to cod.



distribution was similar for male and female plaice in both seasons. The association of plaice with intermediate depths in September was significant for both sexes in 1993 and 1995 but not in 1994 (Table 2). Unlike cod, the association of plaice with deep water in January was highly significant for both sexes in all years (Table 2). January values of *D* tended to be somewhat lower for plaice than for cod. The higher statistical significance of plaice depth associations in January reflects the less aggregated January distribution of plaice compared with cod (Fig. 5).

Like cod, plaice occupied much warmer water in January than in September (Figs. 7 and 8). Median temperatures occupied by plaice were –0.1 to 0.3°C in September and 5.2–5.4°C in January (Fig. 8). Plaice tended to occupy cold temperatures relative to those available in September and warm temperatures relative to those available in January. Male plaice tended to occupy somewhat colder water than females in September but the same temperatures as females in January (Fig. 7). The association between plaice and temperature in September was significant in all three years for males, but was not significant in 1994 and only marginally significant in 1993 for females (Table 2). The association with temperature in January was highly significant in all years for both sexes. The tendency for females to occupy warmer water than males was significant in all three years for September (Table 3: highly significant in 1994 and 1995 for the average and the 90th percentile and significant in 1993 for the median) but in no year for January.

Plaice habitat associations were significant equally often with depth and temperature. The strength of associations also appeared to be similar between the two habitat variables (Table 2). Coordinates of *D* changed between univariate and bivariate tests for both habitat variables in some cases and for neither variable in others. In September tests, female plaice tended to be most strongly associated with depth and male plaice with temperature, based on changes in the coordinates of *D*. In January tests, both sexes appeared to be more strongly associated with depth than with temperature in 1994 and 1995 but not in 1996.

Discussion

Habitat associations of southern Gulf cod and plaice differed markedly between summer and winter, with both species occupying much warmer and deeper waters in winter than in summer. This is generally consistent with the qualita-

© 1998 NRC Canada

Table 1. Habitat associations of southern Gulf of St. Lawrence cod in September and January.

	Depth		Temperature		Depth coordinate (m)		Temperature coordinate (°C)	
Age	*D*	*P*	*D*	*P*	Univariate	Bivariate	Univariate	Bivariate
Sept. 1993	*n* = 183		*n* = 177					
2	51.50	0.0003	45.55	0.0003	55	55	1.5	7.5
3	32.82	0.0007	28.49	0.0017	55	55	1.0	7.5
4	18.95	0.010	15.99	0.055	60	60	1.0	7.0
5	9.93	0.19	12.22	0.070	145	145	0.0	6.5
6	8.57	0.33	15.84	0.010	165	100	0.0	0.0
7+	7.99	0.46	18.56	0.0020	95	100	0.0	0.0
Sept. 1994	*n* = 156		*n* = 152					
2	62.46	0.0003	44.73	0.0003	45	45	1.0	11.0
3	48.19	0.0003	32.89	0.0013	50	50	1.0	10.0
4	32.85	0.0003	21.75	0.0090	50	50	0.5	8.0
5	20.28	0.0003	12.57	0.089	55	55	0.5	8.0
6	15.28	0.0063	10.63	0.13	55	55	0.5	8.0
7+	14.07	0.034	17.78	0.0030	55	115	0.5	0.5
Sept. 1995	*n* = 174		*n* = 174					
2	54.19	0.0003	24.72	0.12	50	50	4.0	9.0
3	44.36	0.0003	28.48	0.0023	50	50	1.0	12.0
4	23.77	0.0017	21.12	0.0057	65	65	0.0	12.0
5	15.95	0.038	15.62	0.038	65	65	0.0	12.0
6	11.14	0.19	11.89	0.13	65	65	0.0	12.0
7+	9.64	0.25	13.21	0.044	50	115	0.0	0.0
Jan. 1994	*n* = 66		*n* = 66					
2	53.69	0.77	47.81	0.63	195	195	5.0	5.0
3	40.65	0.93	43.58	0.60	260	280	4.5	4.5
4	36.98	0.55	42.14	0.26	260	280	4.5	4.5
5	35.35	0.80	61.37	0.016	180	495	5.5	5.5
6	36.77	0.60	65.13	0.0003	220	470	5.5	5.5
7+	38.74	0.40	61.38	0.0003	220	470	5.5	5.5
Jan. 1995	*n* = 128		*n* = 128					
2	46.18	0.062	24.20	0.50	240	240	2.5	6.5
3	40.52	0.16	28.56	0.36	260	260	2.5	6.5
4	35.07	0.42	37.25	0.19	210	270	5.5	5.0
5	42.87	0.19	43.76	0.086	210	435	5.0	5.5
6	44.92	0.12	45.49	0.051	210	430	5.0	5.5
7+	44.83	0.011	44.76	0.0030	210	425	5.0	5.5
Jan. 1996	*n* = 75		*n* = 75					
2	47.82	0.031	30.47	0.23	195	195	5.0	5.0
3	43.03	0.019	23.91	0.26	260	280	4.5	4.5
4	34.30	0.85	53.84	0.11	260	280	4.5	4.5
5	35.68	0.78	51.67	0.13	180	495	5.5	5.5
6	36.62	0.50	39.94	0.19	220	470	5.5	5.5
7+	37.45	0.38	40.80	0.13	220	470	5.5	5.5

Note: *D* is the maximum absolute difference between univariate CDFs of available and occupied habitats, *P* is the significance level of univariate tests of associations with depth and temperature, and *n* is sample size. Coordinates of *D* are given for both univariate and bivariate CDFs.

tive descriptions of the seasonal distributions of these populations in earlier studies (Jean 1964; Powles 1965), although the seasonal shifts reported here appear to be more pronounced than those suggested by the earlier studies. These results for southern Gulf cod and plaice contrast those reported for other groundfish species on the eastern Scotian Shelf (Perry and Smith 1994). On the Scotian Shelf, haddock (*Melanogrammus aeglefinus*) and silver hake (*Merluccius bilinearis*) changed their depth distribution to occupy similar temperatures in both summer and winter whereas yellowtail flounder (*Pleuronectes ferrugineus*) occupied similar depths in both seasons but experienced wide seasonal variation in temperature. Thus, these species appeared to show invariant preferences for either depth or temperature across seasons, in contrast with the marked seasonal variation in apparent preferences for both habitat variables by southern Gulf cod and plaice.

The seasonal changes in habitat associations reported here

© 1998 NRC Canada

Fig. 5. Lorenz curves for age-4 cod and male plaice in September 1993–1995 and January 1994–1996. Each line gives the curve for a single year.

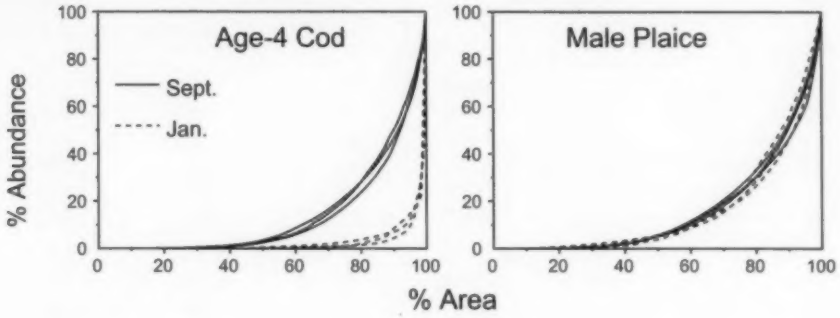
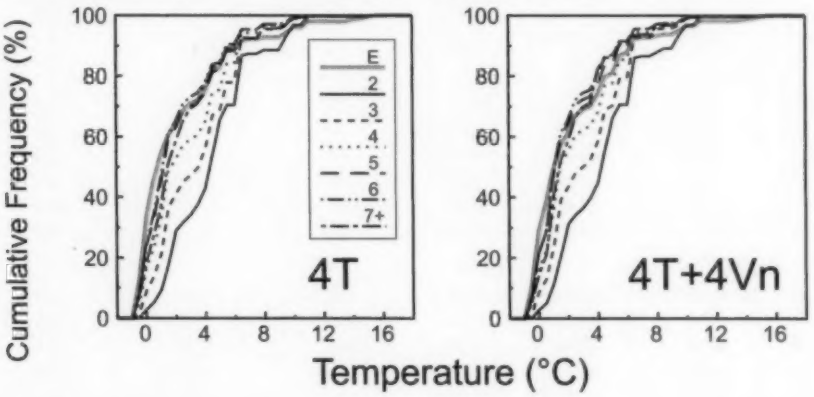
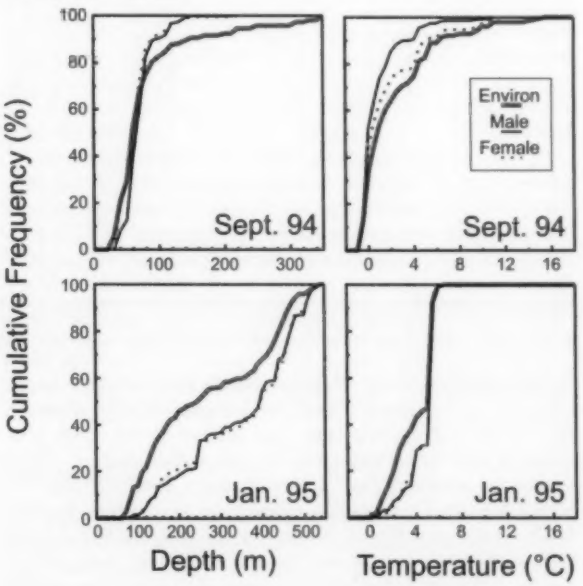


Fig. 6. Cod temperature distribution in September 1994 including or excluding the 4Vn area.



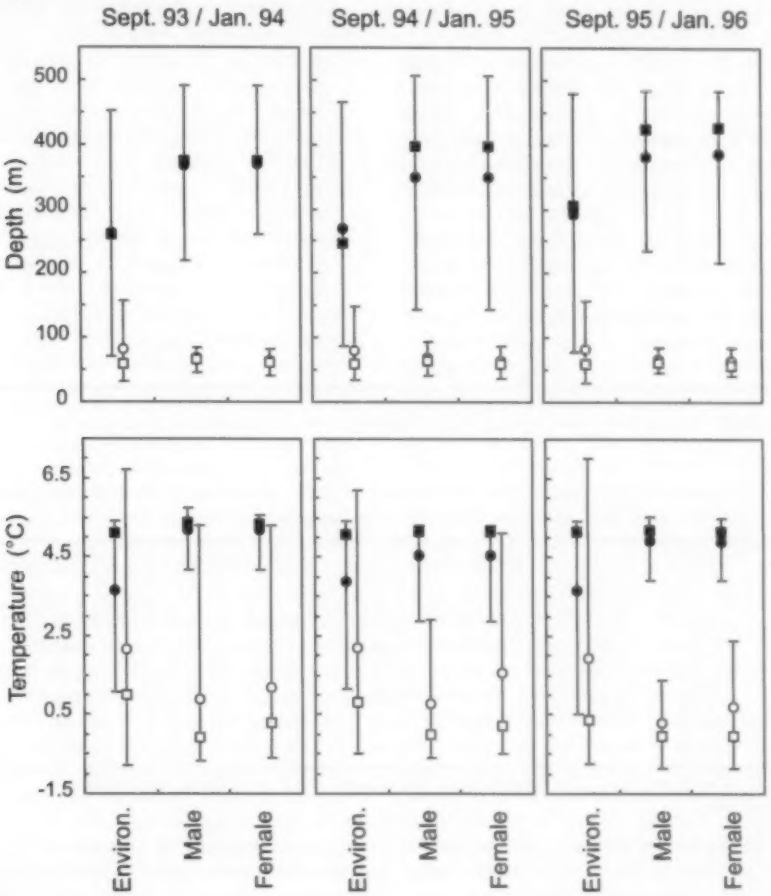
for southern Gulf cod differ from those observed for cod in most other reported cases. Cod on the eastern Scotian Shelf showed only moderate seasonal variation in depth distribution, occupying median depths of 60 m in summer and 115 m in winter–spring (Perry and Smith 1994). Cod showed little seasonal variation in depth distribution on the western Scotian Shelf (Page et al. 1994) and on Georges Bank (Murawski and Finn 1988). In contrast with southern Gulf cod, cod in these more southerly populations occupied warmer temperatures in summer than in winter. Seasonal variation in habitat associations of cod in the northern Gulf of St. Lawrence is more similar to that of southern Gulf cod. Like southern Gulf cod, cod in the northern Gulf occupy deeper and warmer water in winter than in summer (Castonguay et al. 1999). However, the summer habitats reported for northern Gulf cod are much deeper (median occupied depths of 144–181 m) and tend to be warmer (median occupied temperatures of 1.4–3.5°C) than the habitats occupied by cod in the southern Gulf in summer. This difference may partly reflect the large bathymetric difference between the deep northern and shallow southern Gulf (Castonguay et al. 1999) and the more extensive coverage of the available shallows by the southern Gulf survey. Quantitative seasonal comparisons of habitat associations have not been reported for other cod populations. However, northern cod and northeast Arctic cod also undertake migrations between deep wintering areas and shallow summer feeding grounds (e.g., Bergstad et al. 1987; Colbourne et al. 1997) where they are

Fig. 7. Cumulative distributions of plaice catch in relation to depth and temperature for the 1994 September survey of the southern Gulf of St. Lawrence and the 1995 January survey of the Cabot Strait area.



© 1998 NRC Canada

Fig 8. Summary statistics for plaice depth and temperature distributions in September in the southern Gulf of St. Lawrence (open symbols) and in January in the Cabot Strait area (solid symbols). Squares show the median; circles show the average. Lines extend from the 10th to the 90th percentile.



sometimes observed in cold waters (e.g., Woodhead and Woodhead 1965). Thus, northerly cod populations appear to show seasonal variation in habitat associations like those reported here for southern Gulf cod, migrating between deep, warm overwintering grounds and shallow summer feeding grounds where water temperatures may be cold. In contrast, southerly populations, which do not undertake large-scale seasonal migrations (e.g., Martin and Jean 1964), show little seasonal variation in depth distribution and experience the opposite seasonal change in temperature as conditions become warmer in summer. Some northern "stocks" also appear to include a small nonmigratory component that remains inshore in winter where it may experience very cold temperatures (e.g., Jakobsen 1987; Goddard et al. 1994).

Seasonal changes in the habitat associations of southern Gulf plaice are striking compared with those reported for other populations of this species. Murawski (1993) classified plaice off the northeastern U.S. coast as a sedentary deep-water species, exhibiting low variation in seasonal depths and temperatures of occurrence. In this area at the southern limit of their distribution, plaice occupied mean habitats of 135 m and 4.9°C in mid-March and 139 m and 6.2°C in mid-July. Plaice on the northern Grand Banks also showed relatively little seasonal variation in habitat associations (Morgan and Brodie 1991). In this area, plaice were most common at depths between 100 and 200 m and temperatures between –1.1 and –0.5°C in both summer and winter. Distribution on the northern Grand Banks appeared to extend into shallower waters in spring, but plaice were underrepresented in all seasons at temperatures above 1°C. Thus, plaice show extreme variation in seasonal habitat associations among populations, occupying warm water in all seasons off the northeastern U.S. coast and cold water in all seasons on the northern Grand Banks and migrating between cold water in summer and warm water in winter in the Gulf of St. Lawrence.

Environmental variables like temperature, depth, and salinity are all closely linked in these data. Thus, it is difficult to distinguish selection for one particular variable from selection for other correlated environmental variables. Temperature is more likely than depth to be directly important to fish because of its effect on the rates of physiological pro-

© 1998 NRC Canada

Table 2. Habitat associations of plaice in the southern Gulf of St. Lawrence in September and the Cabot Strait in January.

	Depth		Temperature		Depth coordinate (m)		Temperature coordinate (°C)	
Survey	*D*	*P*	*D*	*P*	Univariate	Bivariate	Univariate	Bivariate
Males								
Sept. 1993	18.38	0.0073	19.51	0.0050	50	95	0.5	6.5
Sept. 1994	16.74	0.10	21.05	0.024	50	85	2.0	1.0
Sept. 1995	16.41	0.017	24.10	0.0003	45	90	1.5	2.5
Jan. 1994	37.23	0.0003	35.98	0.0003	245	245	4.0	7.0
Jan. 1995	27.98	0.0017	23.50	0.0047	240	240	3.5	6.5
Jan. 1996	30.01	0.0017	28.55	0.0010	220	220	5.0	5.0
Females								
Sept. 1993	12.87	0.029	11.96	0.054	95	95	0.5	6.5
Sept. 1994	10.97	0.26	9.97	0.36	85	85	0.5	6.5
Sept. 1995	12.55	0.027	17.25	0.0017	90	90	2.5	2.5
Jan. 1994	39.56	0.0003	37.54	0.0007	245	245	4.0	7.0
Jan. 1995	25.61	0.0020	21.04	0.013	240	240	3.5	6.5
Jan. 1996	28.86	0.010	28.92	0.0023	220	220	5.0	5.0

Note: *D* is the maximum absolute difference between univariate CDFs of available and occupied habitats, *P* is the significance level of univariate tests of habitat associations, and sample sizes are as in Table 1 (except $n = 175$ for Sept. 1995). Coordinates of *D* are given for both univariate and bivariate CDFs.

Table 3. Differences between temperature distributions of male and female plaice in the southern Gulf of St. Lawrence in September and in the Cabot Strait in January.

	Average		Median		10th percentile		90th percentile	
Survey	Δ	*P*	Δ	*P*	Δ	*P*	Δ	*P*
S93	0.309	0.062	0.393	0.016	0.093	0.98	0.005	0.52
S94	0.782	0.0003	0.198	0.068	0.099	0.93	2.186	0.0003
S95	0.405	0.0003	0.002	0.97	–0.000	0.99	1.019	0.0003
J94	–0.002	0.96	–0.042	0.054	0.001	0.80	–0.159	0.17
J95	–0.003	0.97	0.000	0.97	–0.000	0.94	–0.003	0.67
J96	–0.008	0.86	–0.011	0.44	–0.002	0.81	–0.046	0.54

Note: Δ is the summary statistic for females minus that for males and *P* is significance according to a randomization test.

cesses (e.g., Fry 1971). However, for most ages of cod, associations in September appeared to be stronger with depth than with temperature. This suggests that depth alone is a better predictor of the determinants of habitat choice by cod in this season than is temperature alone. For example, depth may be a predictor of prey resouces (references in Swain (1993) and Swain and Kramer (1995)), a likely determinant of habitat choice during the summer feeding season. On the other hand, in January when little feeding occurs, older cod appeared to be more strongly associated with temperature than with depth. Thus, seasonal differences appear to occur not just in the habitat occupied by cod, but also in the particular habitat variables that are most strongly associated with cod distribution. Results were more equivocal for plaice. Plaice habitat associations were not consistently stronger with one habitat variable than the other in either season.

While the analyses presented here can provide information on which variable, temperature or depth, appears to be more strongly associated with fish distribution, they cannot address the question of whether significant associations with one variable can be entirely attributed to the association with the other variable. The latter question can be addressed using statistical models relating fish density to habitat variables (e.g., Swain and Morin 1997). In many cases, models containing both depth and temperature terms predicted cod or plaice densities in September in the southern Gulf significantly better than models containing either depth or temperature terms alone (Swain and Kramer 1995; Swain and Morin 1997). This suggests that, at least in summer, cod and plaice associations with either one of these habitat variables cannot be attributed solely to an association with the other variable.

Both cod and plaice from the southern Gulf appeared to avoid cold water in winter but not in summer. The warmer temperature distribution of both species in winter is in contrast with the tendency reported in freshwater fish for low temperature tolerance to be greater in winter than in summer (e.g., Hoar 1955). This result is also opposite to the prediction that colder temperatures should be occupied during the overwintering period than during the summer feeding period, in order to reduce metabolic costs while fasting over winter. Cod and plaice may occupy warm deep waters in winter to avoid freezing. In winter, the Gulf of St. Lawrence is generally ice-covered and temperatures at shallow and intermediate depths may be near the freezing point of seawater (near –1.5°C). Many cold temperate marine teleosts, including Atlantic cod, are capable of producing antifreeze proteins and glycoproteins for protection against freezing in ice-laden seawater (e.g., Fletcher et al. 1987). Antifreeze production in cod (at least in Newfoundland populations) ap-

© 1998 NRC Canada

pears to depend on exposure to cold water, with 1°C required to initiate production and temperatures of 0°C or lower required to maintain it (Fletcher et al. 1987). Thus, in winter, most southern Gulf cod occupy water that is apparently too warm to initiate and maintain antifreeze production. Instead of producing plasma antifreezes, southern Gulf cod and plaice appear to avoid freezing by migrating to warm deep waters. Unless such migrations and the metabolic costs of warm overwintering temperatures are energetically less demanding than the synthesis of plasma antifreezes in winter, it is likely that there are other benefits to this overwintering migration. One possibility is that warm winter temperatures are required for gonad maturation in time for spring spawning (M. Castonguay, Ministère des Pêches et des Océans, Institut Maurice-Lamontagne, C.P. 1000, Mont-Joli, Qué., personal communication). But this explanation does not account for the long-distance migration to areas outside the Gulf because warm water is also available inside the Gulf in the deep waters of the Laurentian Channel.

Differences in temperature distribution between age-classes of cod reversed between September and January. Young cod occupied warmer temperatures than older cod in September and colder temperatures than older cod in January. This reversal reflects wider seasonal variation in temperature distribution for older cod than for young cod. The average temperatures occupied by age-2 cod were similar between September and January whereas those occupied by cod aged 5 years and older were much warmer in January than in September. The wide difference in temperature distribution of older cod between September and January may result from seasonal differences in the factors motivating habitat selection. The tendency for older cod to occupy colder water than younger cod in September may reflect differences between age-classes in a trade-off between the benefits of greater food supplies in warm shallow water versus lower metabolic costs in colder water at intermediate depths (e.g., Swain and Kramer 1995). The strong shift in distribution to warmer water in January for older cod but not for age-2 cod is consistent with the hypothesis that older cod occupy warm water in January to promote gonad maturation as well as with the observation that juvenile cod can be more freeze resistant than adults (Kao and Fletcher 1988). These results also suggest that the opposing ontogenetic shifts in cod habitat associations reported in previous studies reflect a seasonal difference rather than population differences.

Female plaice tended to occupy warmer temperatures than male plaice in September but not in January. The results for September 1993–1995 are consistent with those for September in earlier years (1971–1992), although the differences in September temperature distribution between the sexes tended to decrease as cod abundance increased or plaice abundance decreased (Swain 1997). Swain (1997) proposed an explanation involving a difference between the sexes in the trade-off between foraging rate and predation risk. The higher growth rate of female plaice suggests that the fitness benefits of growth may be greater for females than for males. If so, females would be expected to risk a higher foraging rate than males and consequently obtain a higher food ration. In this case, the optimum temperature for growth would be higher in females than in males, and females would be expected to prefer warmer temperatures than males. The absence of a difference in temperature distribution between the sexes in January is consistent with this hypothesis, since plaice are not feeding in winter.

Seasonal variation may contribute to the differences reported among stocks in interannual changes in distribution. Cod distribution has shifted into deeper water in recent years in the northern Gulf of St. Lawrence (Castonguay et al. 1999) and in Newfoundland waters (Rose et al. 1994) but into shallower water in recent years in the southern Gulf of St. Lawrence (Swain 1999). The shifts into deeper water occurred in late fall and winter whereas that into shallower water occurred in summer – early fall. Thus, the contrast in results between the southern Gulf stock and the stocks in the northern Gulf and Newfoundland waters may reflect seasonal variation in habitat associations and the factors motivating habitat selection. The recent shift to shallow water in the southern Gulf has been coincident with a decline in cod abundance. This is consistent with the hypothesis that the distribution of southern Gulf cod is density dependent during the feeding season, shifting into warm shallow water when abundance is low (Swain 1993; Swain and Kramer 1995). Density-dependent effects on distribution are expected only when fish compete for density-dependent resources like food, and thus may not occur in the late fall and winter when little feeding occurs. The recent shift to deep water in the northern Gulf and Newfoundland waters is coincident with a period of very cold ocean conditions. Southern Gulf cod appear to avoid cold water in winter but not in summer, the season for which interannual variation in their distribution has been described.

Southern Gulf cod and plaice showed striking seasonal differences in habitat associations. These seasonal differences exceeded those observed in most other reported cases for these species. Reasons for these seasonal shifts in habitat preferences and for the marked differences that can occur among populations of the same species in the extent of these seasonal shifts are not well understood. Consideration of these seasonal differences may provide an explanation for apparent differences among cod populations in recent distributional changes. These seasonal differences in habitat associations also need to be considered in bioenergetic analyses of variation in growth and condition (e.g., Krohn et al. 1997).

Acknowledgements

We thank Martin Castonguay for helpful discussion, Fred Page, Martin Castonguay, and two anonymous referees for comments on an earlier draft of this work, and sea-going staff of the Department of Fisheries and Oceans for collecting the data.

References

Bergstad, O.A., Jørgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fish. Res. (Amst.), **5**: 119–161.

Bretherton, F.P., Davis, R.E., and Fandry, C.B. 1976. A technique for objective analysis and design of oceanographic experiments applied to MODE-73. Deep-Sea Res. **23**: 559–582.

© 1998 NRC Canada

Brett, J.R., Shelbourn, J.E., and Shoop, C.T. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. **26**: 2363–2394.

Castonguay, M., Rollet, C., Fréchet, A., Gagnon, P., Gilbert, D., and Brêthes, J.-C. 1999. Distribution changes of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence in relation to an oceanic cooling. ICES J. Mar. Sci.

Clark, D.S., and Green, J.M. 1991. Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*), with evidence supporting an energetic basis for their diel vertical migration. Can. J. Zool. **69**: 1302–1307.

Colbourne, E., deYoung, B., and Rose, G.A. 1997. Environmental analysis of Atlantic cod (*Gadus morhua*) migration in relation to the seasonal variations on the Northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 149–157.

Coutant, C.C. 1987. Thermal preference: when does an asset become a liability? Environ. Biol. Fishes, **18**: 161–172.

Crowder, L.B., and Magnuson, J.J. 1983. Cost-benefit analysis of temperature and food resource use: a synthesis with examples from the fishes. *In* Behavioral energetics: the cost of survival in vertebrates. *Edited by* W.P. Aspey and S.I. Lustick. Ohio University Press, Columbus, Ohio. pp. 189–221.

Dagum, C. 1985. Lorenz curve. *In* Encyclopedia of statistical sciences. *Edited by* S. Kotz and N.L. Johnson. John Wiley & Sons, New York. pp. 156–161.

Fletcher, G.L., King, M.J., and Kao, M.H. 1987. Low temperature regulation of antifreeze glycopeptide levels in Atlantic cod (*Gadus morhua*). Can. J. Zool. **65**: 227–233.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. *In* Fish physiology. Vol. VI. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 1–98.

Gascon, D., Aparicio, M., and Mercille, B. 1990. Estimations du mélange entre les stocks de morue du Nord du Golfe du Saint Laurent (Divisions 3Pn4RS) et les stocks adjacents (2J3KL, 3Ps, et 4TVn [Janvier–Avril]) à partir de résultats de marquage. CAFSAC Res. Doc. 90/61.

Gilbert, D., and Pettigrew, B. 1997. Interannual variability (1948–1994) of the CIL core temperature in the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 57–67.

Goddard, S.V., Wroblewski, J.S., Taggart, C.T., Howse, K.A., Bailey, W.L., Kao, M.H., and Fletcher, G.L. 1994. Overwintering of adult Northern Atlantic cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze glycoprotein levels. Can. J. Fish. Aquat. Sci. **51**: 2834–2842.

Halliday, R.G. 1974. The cod stocks of the southern Gulf of St. Lawrence and Sydney Bight (ICNAF Div. 4TVn). ICNAF Res. Doc. 74/12.

Halliday, R.G., and Koeller, P.A. 1981. A history of Canadian groundfish trawling surveys and data usage in ICNAF Divisions 4TVWX. *In* Bottom trawl surveys. *Edited by* W.G. Doubleday and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 58. pp. 27–41.

Hoar, W.S. 1955. Seasonal variations in the resistance of goldfish to temperature. Trans. R. Soc. Can. Sect. V. Ser. 3, **49**: 25–34.

Jakobsen, T. 1987. Coastal cod in northern Norway. Fish. Res. (Amst.), **5**: 223–234.

Jean, Y. 1964. Seasonal distribution of cod (*Gadus morhua* L.) along the Canadian Atlantic coast in relation to water temperature. J. Fish. Res. Board Can. **21**: 429–460.

Kao, M.H., and Fletcher, G.L. 1988. Juvenile Atlantic cod (*Gadus morhua*) can be more freeze resistant than adults. Can. J. Fish. Aquat. Sci. **45**: 902–905.

Krohn, M., Reidy, S., and Kerr, S. 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 113–121.

Mac, M.J. 1985. Effects of ration size on preferred temperature of lake charr *Salvelinus namaycush*. Environ. Biol. Fishes, **14**: 227–231.

Mahon, R., and Smith, R.W. 1989. Demersal fish assemblages on the Scotian Shelf, Northwest Atlantic: spatial distribution and persistence. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 134–152.

Martin, W.R., and Jean, Y. 1964. Winter cod taggings off Cape Breton and on offshore Nova Scotia banks, 1959–1962. J. Fish. Res. Board Can. **21**: 215–238.

Mohn, R., Lambert, T.C., Wilson, S., and Black, G.A.P. 1997. Update of the status of 4Vn cod: 1996. CSAS Res. Doc. 97/67.

Morgan, M.J. 1993. Ration level and temperature preference of American plaice. Mar. Behav. Physiol. **24**: 117–122.

Morgan, M.J., and Brodie, W.B. 1991. Seasonal distribution of American plaice on the northern Grand Banks. Mar. Ecol. Prog. Ser. **75**: 101–107.

Murawski, S.A. 1993. Climate change and marine fish distributions: forecasting from historical analogy. Trans. Am. Fish. Soc. **122**: 647–658.

Murawski, S.A., and Finn, J.T. 1988. Biological bases for mixed-species fisheries: species co-distribution in relation to environmental and biotic variables. Can. J. Fish. Aquat. Sci. **45**: 1720–1735.

Nakken, O., and Raknes, A. 1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the barents sea, 1978–1984. Fish. Res. (Amst.), **5**: 243–252.

Ottersen, G., Michalsen, K., and Nakken, O. 1998. Ambient temperature and distribution of north-east Arctic cod. ICES J. Mar. Sci. **55**: 67–85.

Page, F.H., Losier, R.J., Smith, S.J., and Hatt, K. 1994. Associations between cod, and temperature, salinity and depth within the Canadian groundfish bottom trawl surveys (1970–1993) conducted in NAFO Divisions 4VWX and 5Z. Can. Tech. Rep. Fish. Aquat. Sci. No. 1958.

Perry, R.I., and Smith, S.J. 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **51**: 589–602.

Powles, P.M. 1965. Life history and ecology of American plaice (*Hippoglossoides platessoides* F.) in the Magdalen Shallows. J. Fish. Res. Board Can. **22**: 565–598.

Rose, G.A., Atkinson, B.A., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 542–552.

Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua* L.) in the southern Gulf of St. Lawrence. ICES J. Mar. Sci.

Sinclair, A. 1992. Fish distribution and partial recruitment: the case of eastern Scotian Shelf cod. J. Northwest Atl. Fish. Sci. **13**: 15–24.

Sinclair, A., Chouinard, G., and Currie, L. 1996. Assessment of the southern Gulf of St. Lawrence cod stock, March, 1996. DFO Atl. Fish. Res. Doc. 96/52.

Smith, S.J., and Page, F.H. 1996. Associations between Atlantic cod (*Gadus morhua*) and hydrographic variables: implications for the management of the 4VsW cod stock. ICES J. Mar. Sci. **53**: 597–614.

Smith, S.J., Perry, R.I., and Fanning, L.P. 1991. Relationships between water mass characteristics and estimates of fish popula-

© 1998 NRC Canada

tion abundance from trawl surveys. Environ. Monit. Assess. **17**: 227–245.

Swain, D.P. 1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 1255–1264.

Swain, D.P. 1997. Sex-specific temperature distribution of American plaice (*Hippoglossoides platessoides*) and its relation to age and abundance. Can. J. Fish. Aquat. Sci. **54**: 1077–1087.

Swain, D.P. 1999. Changes in the distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence: effects of environmental change or change in environmental preferences? Fish. Oceanogr. **8**. In press.

Swain, D.P., and Kramer, D.L. 1995. Annual variation in temperature selection by Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence, Canada, and its relation to population size. Mar. Ecol. Prog. Ser. **116**: 11–23.

Swain, D.P., and Morin, R. 1997. Effects of age, sex and abundance on the bathymetric pattern of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St. Lawrence. J. Fish Biol. **50**: 181–200.

Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. **15**: 393–425.

Wildhaber, M.L., and Crowder, L.B. 1990. Testing a bioenergetics-based habitat choice model: bluegill (*Lepomis macrochirus*) responses to food availability and temperature. Can. J. Fish. Aquat. Sci. **47**: 1664–1671.

Woiwode, J.G., and Adelman, I.R. 1991. Effects of temperature, photoperiod, and ration size on growth of hybrid striped bass × white bass. Trans. Am. Fish. Soc. **120**: 217–229.

Woodhead, P.M.J., and Woodhead, A.D. 1965. Seasonal changes in the physiology of the Barents Sea cod *Gadus morhua* L., in relation to its environment. II. Physiological reactions to low temperatures. ICNAF Spec. Publ. No. 6. pp. 717–734.

© 1998 NRC Canada

Influence of changing food web structure on nutrient limitation of phytoplankton in a highly humic lake

Marko Järvinen and Kalevi Salonen

Abstract: We determined the potential nutrient limitation of summer phytoplankton production using 2 × 2 × 2 factorial design of enrichment bioassays both before and after the introduction of planktivorous whitefish (*Coregonus lavaretus*) in a polyhumic lake with an abundant population of the large cladoceran *Daphnia longispina*. After the fish introduction, *Daphnia* disappeared and was substituted by the rotifer *Keratella cochlearis*. During the dominance of *Daphnia*, additions of nutrients had little or no effect on primary production of phytoplankton in short-term (1-day) incubations. However, 5-day incubations suggested that P most likely was the limiting nutrient. After the fish introduction, both 1- and 5-day enrichment bioassays indicated potential N limitation of phytoplankton production. The strong response of phytoplankton production to combined enrichments with P and N also suggested colimitation by P and N, but this was probably forced by the relatively high additions of nutrients. Consistently low primary production after the combined addition of P and glucose suggests that in the presence of a labile organic C source, epilimnetic bacteria were superior to algae in the uptake of P. Our results suggest that changes in the food web structure may determine the limiting nutrient also in a highly humic lake.

Résumé : Nous avons déterminé la limitation potentielle de la production estivale de phytoplancton par les nutriants au moyen de bio-essais d'enrichissement suivant un plan d'expérience factoriel 2 × 2 × 2 tant avant qu'après l'introduction de corégones planctivores (*Coregonus lavaretus*) dans un lac polyhumique renfermant une population abondante du gros cladocère *Daphnia longispina*. Après l'introduction des poissons, *Daphnia* a disparu et a été remplacé par le rotifère *Keratella cochlearis*. Durant la dominance de *Daphnia*, les additions de nutriants avaient peu d'effet ou aucun effet sur la production primaire de phytoplancton lors d'incubations à court terme (1 jour). Cependant, les incubations de 5 jours ont révélé que le P était très probablement le nutriant limitant. Après l'introduction des poissons, les bio-essais d'enrichissement tant de 1 jour que de 5 jours ont indiqué que la production de phytoplancton pouvait être limitée par le N. La forte réponse de la production de phytoplancton aux enrichissements combinés en P et en N laissent aussi penser qu'il pourrait y avoir co-limitation par ces deux éléments, mais cette forte réponse est probablement en partie attribuable aux additions relativement importantes de nutriants. La production primaire toujours faible observée après l'addition combinée de P et de glucose laisse penser qu'en présence d'une source de C organique labile, les bactéries épilimniques absorbaient davantage de P que les algues. Nos résultats indiquent que les changements dans la structure du réseau alimentaire peuvent aussi déterminer le nutriant limitant dans un lac hautement humique.

[Traduit par la Rédaction]

Introduction

Phosphorus (P) and nitrogen (N) commonly limit phytoplankton growth in aquatic ecosystems (Hecky and Kilham 1988). In freshwater, P is generally considered to determine the potential algal primary production. However, depending on P and N inputs from the catchment, sediment, and atmosphere (e.g., Levine and Schindler 1992) and nutrient recycling in the water (Schindler et al. 1993; Vadstein et al. 1993; Sterner and Hessen 1994), the nutrient that limits algal growth may vary on a temporal and spatial scale in lakes (e.g., Elser et al. 1995*a*).

Zooplankton act as both a link and a sink in nutrient cycling in lakes and can modify the nutrient availability for algae (e.g., Sterner and Hessen 1994). Zooplankton affect phytoplankton directly through grazing and nutrient excretion. Because the nutrient stoichiometry of zooplankton varies between the species, the recycling efficiency of a nutrient may depend on a zooplankton assemblage (Sterner and Hessen 1994). Owing to their higher proportion of P, the N:P ratio of released nutrients of large daphnids is generally higher than that of copepods (Sterner and Hessen 1994). The dominance of daphnids may thus contribute to P deficiency of phytoplankton. As a whole, the role of zooplankton in nutrient dynamics is important, since they may be the largest particulate nutrient pool (e.g., Hessen et al. 1992) in many lakes.

Fish also play an important role in nutrient cycling in lakes (Carpenter et al. 1992). Fish can recycle large amounts of P, but because they are a major pool of P in many lakes (e.g., Kitchell et al. 1975), they may also be a sink for P (Carpenter et al. 1992). Predation by planktivorous fish may

Received January 9, 1997. Accepted September 2, 1998.
J13826

M. Järvinen[1] and K. Salonen. University of Helsinki, Lammi Biological Station, FIN-16900 Lammi, Finland.

[1]Author to whom all correspondence should be addressed.

© 1998 NRC Canada

alter the size structure and biomass of zooplankton and thereby indirectly affect nutrient cycling (Carpenter et al. 1992). Correspondingly, introduction of fish often has cascading effects on aquatic ecosystems (Threlkeld 1987).

In brown-water lakes, high concentrations of dissolved organic matter (DOM) affect P availability and transformations (Jones 1992). Dissolved inorganic P (DIP) forms complexes with dissolved humic matter and iron, which may reduce P supply for plankton (Jones 1992). Conversely, P can be released from these complexes under depletion of free DIP in water or by ultraviolet light. Due to a high proportion of dissolved organic nutrients in the total nutrient pool of humic lakes (Salonen et al. 1994), total nutrients seem to be poor predictors of the trophic state (Jones 1992) or nutrient limitation (Jones 1990) in these lakes.

We have studied the importance of the food web structure as a modifier of nutrient cycling in polyhumic Lake Mekkojärvi in southern Finland. In the summer of 1994, planktivorous whitefish (*Coregonus lavaretus*) fingerlings were introduced into the lake to remove the dominating large cladoceran *Daphnia longispina*. Because a large proportion of epilimnetic particulate P can be found in *Daphnia* (Salonen et al. 1994), we hypothesized that its removal and replacement by other zooplankton species would release phytoplankton production from apparent P limitation. Here, we report the results of the enrichment bioassays, which were carried out to determine nutrient(s) that potentially limited primary production of phytoplankton before and after the food web manipulation.

Material and methods

Study site

The study was conducted in small (area 0.35 ha), shallow (z_m 3.5 m), acidic (pH 5.2–6.5) Lake Mekkojärvi in southern Finland (25°3′E, 61°13′N). The lake is strongly coloured (300–600 g Pt·m^{-3}) by high humic inputs (Salonen et al. 1992). The shoreline of the lake is surrounded by floating *Sphagnum* and *Warnstorfia* mosses and there is no shallow littoral area. After ice-break, usually in early May, water warms up rapidly, leading to a steep thermal and chemical stratification (Salonen et al. 1992). As a result, the trophogenic layer is limited to the upper 0.5–1 m and mineral nutrients (PO_4^{3-}, NO_3^-, NH_4^+) are often depleted in the shallow epilimnion.

In Lake Mekkojärvi, the species richness of plankton is low and its carbon (C) flow is largely based on allochthonous organic matter (Salonen et al. 1992). With an exception of a few northern pike (*Esox lucius*), which prey on amphibians and aquatic insects, the lake was fishless at the beginning of the study. In the summer, zooplankton biomass is almost exclusively formed by the cladoceran *D. longispina* (Kankaala 1988). In the absence of planktivorous fish, *D. longispina* effectively grazes on bacterio- and phytoplankton (Kankaala 1988; Salonen et al. 1992). Up to 85% of the epilimnetic particulate P in Lake Mekkojärvi may be bound in *Daphnia* (Salonen et al. 1994).

Food web manipulation

One thousand individuals (2860 ind.·ha^{-1}) of 0+ whitefish fingerlings 4–6 cm in length were introduced into the lake on 14 July 1994. P and N contents of fish tissue were 3.12 and 9.36% of dry mass, respectively. Accordingly, introduced fish contained 0.22 mmol P·m^{-2} and 0.67 mmol N·m^{-2}. Anoxia in the deeper water layers of Lake Mekkojärvi restricted the vertical distribution of whitefish to the upper 0.6–0.9 m of the lake.

Nutrient enrichment bioassays

Nutrient enrichment bioassays were conducted weekly during June–August 1994. Duplicate samples from depths of 0, 0.25, and 0.5 m, representing the epilimnion, were collected from the middle of the lake in a 15-L polyethylene container with a 0.3-m-long tube sampler (Limnos Ltd., Finland). Large zooplankton and their invertebrate predators were removed by screening the sample water through a 200-μm-mesh net. The container was closed with a screwcap with a silicone subsampling tube, mixed, and enclosed in a black polythene bag.

An acid-washed 0.5-L polyethylene bottle was filled with the sample water for the determination of ambient nutrient (N and P) concentrations. Then, for each day of the experiment, two acid-washed and preignited 20-mL glass scintillation vials were filled with sample water. At least twice the vial volume was allowed to overflow before stoppering, and no airspace was left in the vials. The subsamples were stored in darkness until all vials were filled. To leave an airspace for subsequent nutrient, radiocarbon, and formaldehyde additions, 0.30 mL of sample water was pipetted out of the vials just before the additions.

P (KH_2PO_4), N (NH_4Cl), and C (α-D(+)glucose) were added separately and in all combinations in a 2 × 2 × 2 factorial design to final concentrations of 1.6 μmol P·L^{-1}, 25.0 μmol N·L^{-1}, and 41.7 μmol C·L^{-1}, respectively. The enrichments followed the N:P ratio of 16:1 (by atoms). In addition to NH_4-N, enrichments with NO_3-N as KNO_3 (on 22 June and 10 August) and urea ($CO(NH_2)_2$) (on 6 July and 17 August) at final N concentrations of 25.0 μmol·L^{-1} were carried out to study responses of phytoplankton to various species of N. Biological activity in stock solutions was inhibited by autoclaving.

An initial total N to total P (TN:TP) atomic ratio of 49–123:1 changed after P and P plus C additions to 13–22:1, after N and N plus C additions to 90–219:1, and after P plus N and P plus N plus C additions to 25–33:1. The concentrations of dissolved free carbohydrates (DFCHO) vary between 1 and 50 μg·L^{-1} in Lake Mekkojärvi (Münster et al. 1992). Therefore, the addition of glucose increased the DFCHO pool more than 10-fold. However, C enrichment had a minor effect on the total epilimnetic dissolved organic C (DOC) pool of Lake Mekkojärvi, which was 0.83–1.0 mmol·L^{-1} during June–August 1994.

After nutrient additions, 10 μL of $Na_2{}^{14}CO_3$ solution (3.7 × 10^5 Bq·mL^{-1}) was pipetted into the vials. The samples were incubated in situ in a transparent rack at a depth of 0.25 m, where primary production of phytoplankton is about 50% of that at the surface. Phytoplankton production was first measured 1, 2, and 5 days after the additions, but after the second experiment the 2-day incubation was omitted. The incubations of primary production were terminated in the field with 0.2 mL of 40% formaldehyde. [^{14}C]Bicarbonate uptake in the light (without a dark bottle correction) was measured by the acidification and bubbling modification of the ^{14}C method (Schindler et al. 1972). Samples were counted with a Wallac 1409 scintillation counter. Primary productivities measured in duplicate vials generally were similar, but in some cases the difference between the replicates was high due to a leakage of the screwcaps of some vials. The exceptionally low replicate values (13 out of the 270) were therefore discarded. Four additional water samples, distributed evenly within the series of water samples taken for the nutrient limitation bioassay, were taken into scintillation vials for the determination of dissolved inorganic C (DIC) with a C analyzer (Salonen 1981). The concentration of DIC was 0.20–0.32 mmol·L^{-1} in June–August 1994.

Chemical determinations

Samples for the determination of soluble reactive P (SRP) and NO_2+NO_3-N were filtered through 0.2-μm Millipore Millex GS filters, first rinsed with deionized and lake water, immediately upon returning to the laboratory. After filtration, the samples were

© 1998 NRC Canada

Table 1. Characteristics of Lake Mekkojärvi water in the uppermost 0.5 m during June–August 1994.

SRP ($\mu mol \cdot L^{-1}$)	NH_4-N ($\mu mol \cdot L^{-1}$)	NO_2+NO_3-N ($\mu mol \cdot L^{-1}$)	DIN ($\mu mol \cdot L^{-1}$)	TP ($\mu mol \cdot L^{-1}$)	TN ($\mu mol \cdot L^{-1}$)	POP ($\mu mol \cdot L^{-1}$)	PON ($\mu mol \cdot L^{-1}$)	DIC ($mmol \cdot L^{-1}$)
0.04±0.03	0.15±0.09	0.72±0.16	0.86±0.21	0.44±0.15	37.4±6.5	0.24±0.13	4.04±1.59	0.26±0.04
(0.03–0.13)	(0.07–0.21)	(0.50–1.21)	(0.71–1.43)	(0.26–0.87)	(28.8–53.6)	(0.10–0.55)	(2.29–8.86)	(0.20–0.32)

Note: Values are means ± SD (n = 28). Minimum and maximum values are given in parentheses. SRP, soluble reactive P; DIN, dissolved inorganic N ($NO_2+NO_3+NH_4$); TP, total P; TN, total N; POP, particulate organic P; PON, particulate organic N; DIC, dissolved inorganic C.

frozen to await further analysis together with the unfiltered water samples for the determination of TP and TN. NH_4-N was determined immediately after returning to the laboratory according to the modification of Solórzano (1969). SRP and NO_2+NO_3-N were determined with an AKEA autoanalyzer according to Murphy and Riley (1962) and Wood et al. (1967), respectively. TP and TN were determined after alkaline persulphate digestion (Koroleff 1983). Dissolved TP and TN were determined similarly from preignited Whatman GF/F filtrates, and dissolved organic P (DOP) and N (DON) were calculated as a difference between dissolved total and inorganic nutrients. Four pieces of known area of glass fibre filters were also punched for the determination of particulate organic N (PON) and P (POP). The results of particulate organic nutrients were not corrected for detrital contribution. For the assessment of nutrient contents of zooplankton, 15–106 randomly selected individuals of *Daphnia* were collected with forceps, or 30 individuals of *Keratella* distributed in deionized water with a capillary pipette, into acid-washed glass scintillation vials. The samples were dried at 60–65°C for a day and N and P determined after the addition of deionized water and persulphate digestion. The biomass of the *Keratella* population was estimated using a mean individual C content of 0.024 µg C·ind.$^{-1}$ (Latja and Salonen 1978). For the *Daphnia* population, we used a mean value of 6.85 µg C·ind.$^{-1}$, based on C determinations of the individual *Daphnia* from Lake Mekkojärvi between late May and mid-July 1984 (A. Ojala, Department of Ecological and Environmental Sciences, University of Helsinki, personal communication). Nutrient contents of fish were assessed from the samples of 4–16 whitefish caught on five occasions between August and October 1994. Frozen fish samples were allowed to thaw and weighed (fish plus thaw water) to the nearest 0.001 g (wet mass). Fish were then dried for a week at 60–65°C and reweighed to obtain dry mass. The procedure was repeated to confirm the dry mass estimates. Fish were then pulverized into a fine powder with a mortar and pestle. Pulverized fish samples were again dried at 60–65°C, whereafter subsamples were mixed with deionized water and analyzed for N and P concentration (per unit mass) using the same method as for total nutrients. Temperature and dissolved oxygen were measured in situ with a combined probe (Yellow Springs Instruments, Ohio) in the middle of the lake.

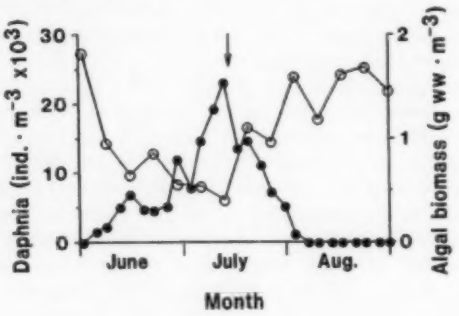
Statistical analyses

The main effects (nutrient enrichment, food web manipulation, and nutrient enrichment × food web manipulation interactions) and the time trends (within-subject effects) were studied using model I two-way analysis of variance (ANOVA) with repeated measures (SYSTAT 5.0). Significant main (between-subject) effects were examined with appropriate linear contrasts with a multivariate F statistic (Wilks' lambda). For the ANOVA, the missing data of the 5-day incubations on 6–11 June 1994 were extrapolated from the results of the 2-day incubations of the same experiment.

Results

Following the introduction of whitefish fingerlings in the middle of July, the population of *D. longispina* rapidly declined and was virtually eliminated by the beginning of August (Fig. 1). After the collapse of the *Daphnia* population, the rotifer *Keratella cochlearis* became the dominant zooplankton species. Between the dominance of these two species, at the beginning of August, zooplankton biomass was very low. The biomass peak of the *Keratella* population (0.07 g C·m^{-3}) in the middle of August was lower than that of *Daphnia* in the middle of July (0.16 g C·m^{-3}).

Fig. 1. Density of *D. longispina* (solid circles) and total biomass of phytoplankton (open circles) in the epilimnion of Lake Mekkojärvi in the summer of 1994. The arrow indicates the time of whitefish introduction.



Physical and chemical properties of the epilimnion

During the summer of 1994, Lake Mekkojärvi was steeply stratified. In June and late August, the epilimnion was about 1 m deep, but during the warm period in July and early August, it was restricted to the upper 0.6 m.

The epilimnetic concentration of inorganic P was around the limit of the detection of the molybdate method, and the concentration of NH_4-N was also very low (Table 1). In the dissolved inorganic N (DIN) pool, NO_2+NO_3-N clearly dominated. Besides other serious limitations of using the N:P ratio of inorganic nutrients (e.g., Hecky and Kilham 1988), the observed low concentrations made such ratios useless. The epilimnetic concentration of TN was highest (42.8–53.6 µmol·L^{-1}) in early June and steadily decreased towards late summer. The concentration of TP was highest (0.52–0.87 µmol·L^{-1}) in early June and late August and showed little variation from mid-June to mid-August. DON comprised 78–98% of the TN pool, while the respective proportion of DOP was lower, 31–88%. Within the uppermost 0.5 m of Lake Mekkojärvi, nutrients were rather uniformly distributed. Higher concentrations of total nutrients were found in the anoxic hypolimnion (results not shown). The atomic TN:TP ratio in the epilimnion was always >40 and suggested P limitation of phytoplankton (Fig. 2A). However, the TN:TP ratio increased in June and early July, while after the fish introduction the ratio showed quite a consistent de-

© 1998 NRC Canada

Fig. 2. (A) Ambient total nutrient ratio of Lake Mekkojärvi water and (B) N:P ratio of seston in the epilimnion during the study. The broken line is the N:P ratio of 16:1. The arrow indicates the time of whitefish introduction.

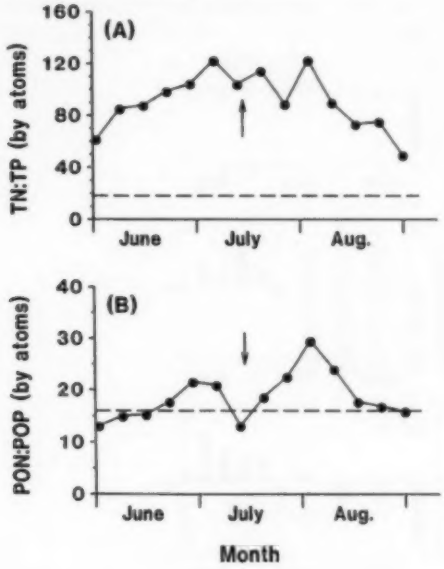
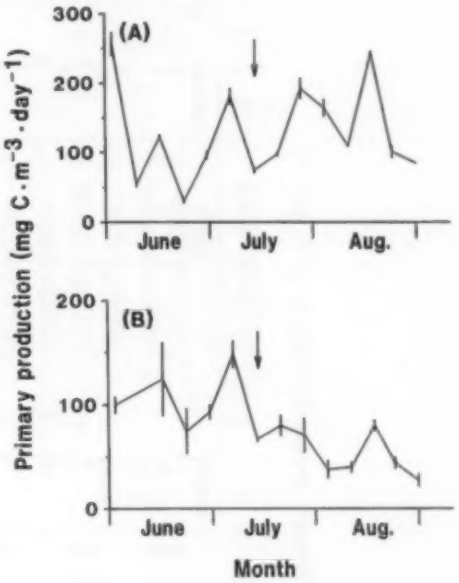


Fig. 3. Mean phytoplankton production (with the range of two replicates) in the untreated controls during the study: (A) 1-day incubations; (B) 5-day incubations. The results of 5-day incubations are shown as a daily rate. The arrow indicates the time of whitefish introduction.



creasing trend, suggesting a relaxation of P limitation. The N:P ratio of seston (mean 16.7, by atoms, n = 7) in the epilimnion indicated balanced nutrient availability before the fish introduction. Later, the ratio increased and reached a value of 29.5 at the same time as *Daphnia* disappeared but was not yet replaced by other species (Fig. 2B). Along with the increase of the *K. cochlearis* population, the ratio returned to the values of the balanced nutrient level. The increase in the N:P ratio of seston resulted from the higher concentrations of PON (cf. Table 1) after the fish introduction (mean 4.4 µmol·L^{-1}, n = 7) than before it (mean 3.7 µmol·L^{-1}, n = 7). The median N:P content of *K. cochlearis* was 22.0 (8.3–40.5, approximate 95% confidence limits, n = 20), while the respective value for *D. longispina* was 2.7 (2.4–3.8, n = 25).

Plankton communities in the epilimnion

With the exception of early June, when dinoflagellates contributed markedly to the total biomass of phytoplankton, chrysophytes and cryptomonads generally formed >80% of the total algal biomass in the epilimnion of Lake Mekkojärvi. The flagellated species belonging to the genera *Cryptomonas*, *Mallomonas*, and *Uroglena* dominated biomass throughout the summer (unpublished results). Omitting the highest phytoplankton biomass on 1 June 1994, which still reflected the wane of the spring bloom, the phytoplankton biomass doubled after the fish introduction (Fig. 1). Total protozoan biomass in the epilimnion also increased three- to nine-fold after the fish introduction (unpublished results). The increase was particularly pronounced in the numbers of ciliates and choanoflagellates. The change in the protozoan community was most distinct from the beginning of August, thus coinciding with the complete disappearance of *Daphnia* from the lake.

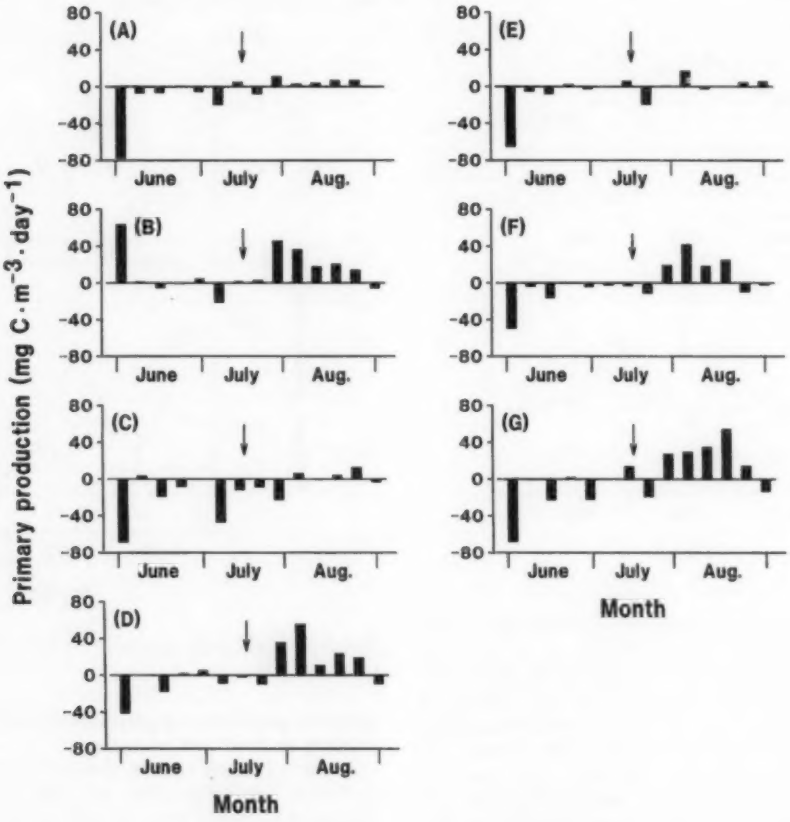
Nutrient limitation of phytoplankton production in relation to food web changes

In the untreated control samples, phytoplankton production after 1 day fluctuated throughout the summer, but on average was higher after the introduction of fish (Fig. 3A). The same trend was observed in our weekly in situ determinations of primary production, done at the same depth over 24 h in 100-mL glass bottles without the removal of large zooplankton (unpublished results). In the control vials of 5-day incubations, primary production decreased towards the end of summer (Fig. 3B).

Before the fish introduction, nutrient enrichments generally had little or no effect on phytoplankton production after 1 day (ANOVA, p values from 0.162 to 0.831, df = 7, 10, n = 32) (Figs. 4 and 5A). The only significant difference was found in C enrichments, which decreased primary production (p = 0.003). After the fish introduction, single P enrichments continued to have little effect on primary production (p = 0.997) (Fig. 4A). Two weeks after the fish introduction, when the density of *Daphnia* collapsed (cf. Fig. 1), phytoplankton production consistently increased in all N enrichments, and this situation persisted for 1 month (Fig. 4). The increase was significant with N, P plus N, and N plus C enrichments (p = 0.004, 0.001, and 0.039, respectively) (Fig. 5A) but, despite the similar appearance of the results, not with P plus N plus C enrichment (p = 0.186). However, after the fish introduction, all treatments with N had a higher mean production (154–161 mg C·m^{-3}, n = 14) than treatments without N (136–145 mg C·m^{-3}, n = 14) (Fig. 5A). Be-

© 1998 NRC Canada

Fig. 4. Responses of phytoplankton production to nutrient enrichments in 1-day incubations in Lake Mekkojärvi. Control values were subtracted from the results. (A) PO_4^{3-} addition; (B) NH_4^+ addition; (C) glucose addition; (D) PO_4^{3-} plus NH_4^+ addition; (E) PO_4^{3-} plus glucose addition; (F) NH_4^+ plus glucose addition; (G) PO_4^{3-} plus NH_4^+ plus glucose addition. The arrow indicates the time of whitefish introduction.



cause there was no significant difference (p = 0.108) between the effects of a single and combined additions, N alone mostly was responsible for the stimulation of primary production in 1-day incubations following the fish introduction.

The results of 5-day incubations were different. The results were generally less variable than those of 1-day incubations because during the longer time interval the differences between the treatments and controls grew larger. From June to mid-July, when *Daphnia* was abundant, primary production increased in water enriched with P, P plus N, and P plus N plus C (p values <0.001) (Figs. 5B and 6), suggesting P deficiency. However, after mid-July, P enrichments alone had no effect on primary production (p = 0.914), while respective enrichments with N increased it (Figs. 5B and 6). Although the increase was significant (p < 0.001) only in water enriched with P plus N and P plus N plus C, enrichments with N and N plus C also increased primary production (p = 0.255 and 0.586, respectively) (Fig. 5B). The colimitation by P and N was obvious already in June, although its maximum occurred only after the fish introduction (Fig. 6). As in 1-day experiments, nutrient additions had no effect on primary production at the end of August. P plus C enrichment always resulted in lower phytoplankton production than in the control, although the difference was not significant (p = 0.827).

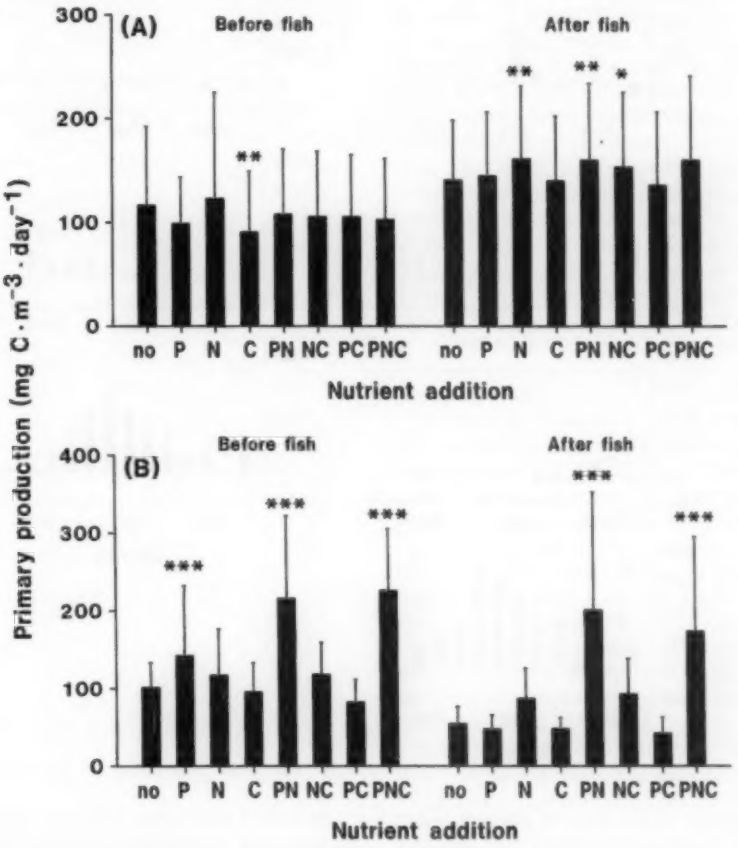
Phytoplankton production responded similarly to enrichments with various species of N in 1- and 5-day incubations (p values from 0.074 to 0.834, df = 1, n = 16). In 1-day experiments, primary production was slightly higher after NH_4^+ amendment than after NO_3^- or urea amendment (all results below the 1:1 line, Fig. 7A). In 5-day incubations, all three N sources resulted in rather similar primary production (Fig. 7B).

Discussion

In Lake Mekkojärvi, the large cladoceran *D. longispina* has regularly dominated the zooplankton community from June to late autumn since the first zooplankton observations made in the year of 1984 (Kankaala 1988; Salonen et al. 1994; and unpublished observations). The collapse of the *Daphnia* population started immediately after the fish introduction (Fig. 1). Conversely, in the isolated 2-m-diameter water columns in the lake (unpublished results), *Daphnia* survived late in the autumn. This strongly suggests that in

© 1998 NRC Canada

Fig. 5. Mean phytoplankton production (± SD) in the nutrient bioassays in Lake Mekkojärvi before (1 June – 14 July 1994) and after (14 July – 31 August 1994) the introduction of whitefish. (A) Primary production 1 day after enrichments; (B) primary production 5 days after enrichments (shown as a daily rate); $n = 14$ for all experiments, except for P on day 1 before fish introduction and N, N plus C, P plus C, and P plus N plus C on day 5 before fish, when $n = 13$, and for control (no enrichments) on day 5 before fish introduction, when $n = 12$. Significance was determined by ANOVA using multivariate F-tests as compared with control values: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.



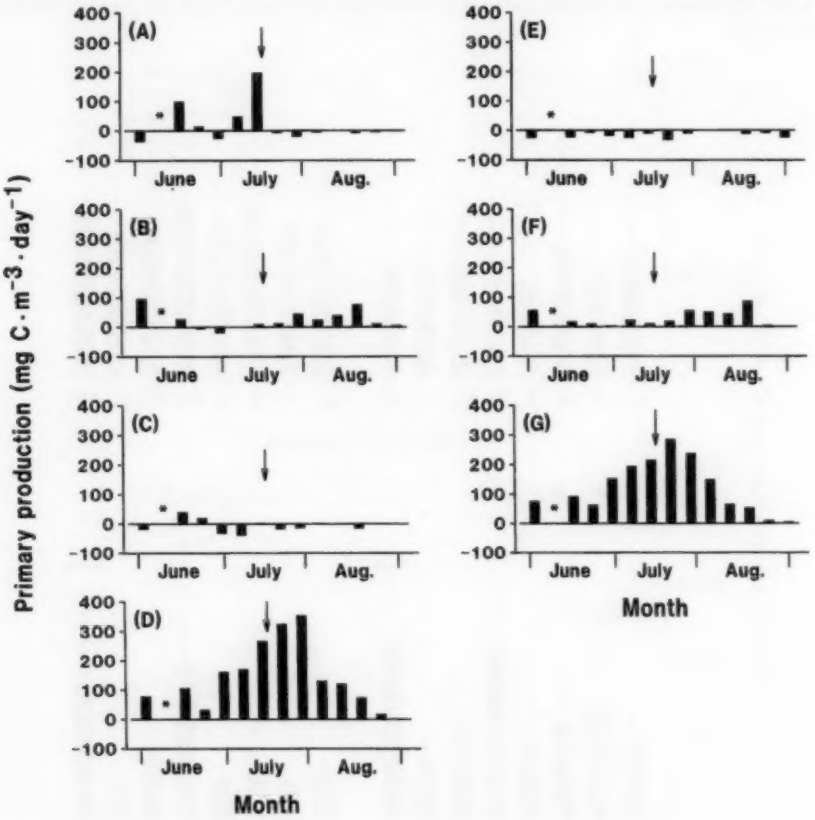
Lake Mekkojärvi, whitefish predation caused the shift from the dominance of *Daphnia* to the dominance of rotifers.

Due to its small area and sheltered position, Lake Mekkojärvi has no waves and the throughflow is generally low. Low turbulence leads to a rapid sedimentation of nonliving particles out of the shallow and often very warm epilimnion. Therefore, seston of Lake Mekkojärvi is probably mostly composed of living particles and corresponds to the stoichiometry of plankton. Since the sampling and handling practices of chemical samples typically underrate larger zooplankton, our seston results mainly refer to phytoplankton, protozoans, and rotifers. The slight increase in the particulate N:P ratio suggests that P became more limiting along with the decrease of the *Daphnia* population, which was against expectations based on its high P content (median N:P ratio of 2.7). Although the changes in the seston N:P ratio seemed clear and logical, it is difficult to interpret these results with certainty because we did not differentiate nutrient ratios at the species or group level. Makarewicz and Likens (1979) found that N and P contents in rotifers were similar to those in calanoid copepods, i.e., they tended to have higher N levels than large cladocerans (Sterner and Hessen 1994), which was also found in this study (the median N:P ratio of 22). This might to some extent explain the observed changes in the seston N:P ratio of Lake Mekkojärvi.

In contrast with the seston N:P ratio, which suggested the appearance of P limitation along with the decrease of *Daphnia*, the 1-day nutrient enrichments suggested the appearance of N limitation. The results of 5-day experiments suggested the same, but the main effect was colimitation by N and P, which was strong already before the fish introduction. N limitation may be explained by intensified P recycling after the disappearance of *Daphnia*. The massive addition of whitefish alone might at least partly explain the relaxation of P deficiency, since in planktivore-dominated systems, excretion by young fish may dominate P recycling (Schindler et al. 1993; Vanni et al. 1997). The role of whitefish in the nutrient recycling may have been more important immediately after their introduction into Lake Mekkojärvi, since at that

© 1998 NRC Canada

Fig. 6. Responses of phytoplankton production to nutrient enrichments in 5-day incubations in Lake Mekkojärvi. Control values were subtracted from the results. The results of 5-day incubations are shown as a daily rate. (A) PO_4^{3-} addition; (B) NH_4^+ addition; (C) glucose addition; (D) PO_4^{3-} plus NH_4^+ addition; (E) PO_4^{3-} plus glucose addition; (F) NH_4^+ plus glucose addition; (G) PO_4^{3-} plus NH_4^+ + glucose addition. The arrow indicates the time of whitefish introduction; *no data due to missing controls.

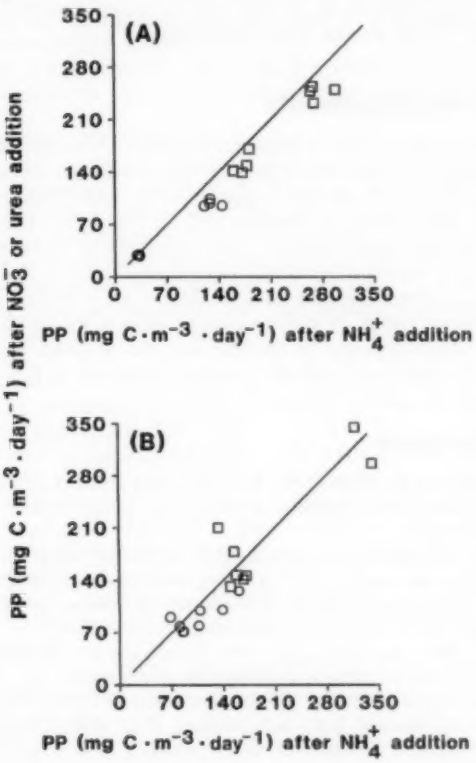


time, they had an abundance of *Daphnia* to prey on. After the disappearance of the *Daphnia* population, fish probably starved, which is supported by the fish biomass results indicating that in late October, young whitefish had the same biomass as at the beginning of August. The sedimentation of particulate P (e.g., feces of fish) was probably rapid from the shallow (<1 m) and nonturbulent epilimnion of Lake Mekkojärvi, and therefore, feces of fish likely had a minor role in the availability of epilimnetic P. Thus, it is probable that sedimentation increased in the epilimnion after the disappearance of *Daphnia*, since during the dominance of *Daphnia*, its diffuse feces probably remained in the epilimnion. Along with rotifers, protozoans also increased in numbers in the epilimnion of Lake Mekkojärvi after the collapse of the *Daphnia* population (unpublished results). The central role of heterotrophic nano- and micro-zooplankton on nutrient regeneration in freshwater is well documented (Porter et al. 1979). Particularly, protozoans seem to release more P than herbivorous macrozooplankton (Vadstein et al. 1993). Thus, the severalfold increase of the protozoan biomass after the fish introduction also likely contributed to the relaxation of P limitation in the epilimnion of Lake Mekkojärvi, at least during incubations in the vials.

In Lake Mekkojärvi, however, it is an oversimplification to look only at nutrient concentrations in the epilimnion. In the lake, phytoplankton migrates vertically with a diel cycle, and algae retrieve nutrients from the hypolimnion, which could directly be seen as a decrease in hypolimnetic nutrient concentrations (unpublished results). This alone would mean that 5-day nutrient enrichment experiments might yield invalid results because the hypolimnetic, "naturally" existing source of nutrients is excluded. For 1-day experiments, this source of error may have been less important, although even then, phytoplankton successively experienced more than two times longer a light period than in the lake, which may also have led to unrealistic depletion of nutrients. Further, we do not know the N:P ratio of inorganic nutrients in the hypolimnion because in the study year, as a result of the increased phytoplankton biomass after the fish introduction, nutrients were exceptionally depleted down to the deepest sampling depth of 2 m, which might also explain the migration of *Cryptomonas* cells below 2 m depth during night in August (unpublished results). It seems clear, however, that the rapid uptake and high storage capacity of P by phytoplankton might alone lead to the lower N:P ratio of algae, if this nutrient is retrieved in darkness by vertical migrations.

© 1998 NRC Canada

Fig. 7. Relationship between primary production (PP) after NH_4^+ enrichment and primary production after NO_3^- enrichment (circles) or urea enrichment (squares) in the bioassays carried out in Lake Mekkojärvi in 1994. The solid line represents the 1:1 line. (A) Primary production after 1 day; (B) primary production after 5 days. The results of 5-day incubations are shown as a daily rate.



Although the total biomass of phytoplankton increased after the fish introduction, the algal community structure mostly remained similar during the study period. As a result, the absolute biomasses of the dominating algal species *Cryptomonas* and *Mallomonas* increased, and since particularly the former species migrated into the deeper water layers (unpublished results), there is a possibility that their refueling of internal cellular stores in the hypolimnion contributed at least to some extent to the more potential epilimnetic N limitation. The increase in algal biomass after the fish introduction also remarkably increased the overall need for mineral nutrients in the epilimnion of Lake Mekkojärvi.

Bacterivory by algae may also be an important strategy for acquiring P or other nutrients in short supply (Nygaard and Tobiesen 1993), and in humic lakes, high bacterial numbers induced by high inputs of allochthonous organic matter may promote this strategy (Jansson et al. 1996). During this study, phytoplankton assemblage in the epilimnion consisted of many species also capable of phagotrophy (unpublished results). Salonen et al. (1994) found that in Lake Mekkojärvi, both bacterial (0.2–1.0 µm) and phytoplankton (1–50 µm) size fractions had nearly a similar affinity to take up PO_4^{3-} from water. This relatively fast uptake by the algal size fraction was tentatively attributed to flagellates grazing on bacteria.

Systematically high primary production after combined P and N amendments suggested tight coupling between P and N in Lake Mekkojärvi, particularly in July. This agreed with the results of Jones (1990), obtained during the dominance of *D. longispina*, that in Lake Mekkojärvi, phytoplankton "generally experience a restricted but approximately balanced nutrient supply and hence do not respond to an increase in the availability of a single nutrient." A similar kind of colimitation of phytoplankton by P and N has recently been reported from a variety of lakes (e.g., Elser et al. 1990). However, it is likely that in our study the colimitation was forced by the conditions of the experiment, i.e., the nutrient additions were high relative to the concentrations in the lake, which led to colimitation, and therefore the sensitivity of the phytoplankton response to the primary limiting nutrient remained partly obscured. For example, Schelske et al. (1986) have shown that even small nutrient spikes can stimulate phytoplankton responses. It is likely that factors other than P and N limited the responses of phytoplankton in Lake Mekkojärvi when P and N were added together. True tests for colimitation would have required a different experimental design (e.g., Hecky and Kilham 1988).

The failure of P plus C additions to increase phytoplankton production during 5-day incubations is interesting and suggests that in the presence of a labile organic C source, bacteria were superior to algae in the uptake of P. Earlier results from Lake Mekkojärvi have shown that bacterioplankton dominate P uptake (Jones 1990; Salonen et al. 1994), although phytoplankton may successfully compete with bacteria for available P (Jones 1990). Recent studies have shown that bacterial growth may be more limited by P than by C (e.g., Elser et al. 1995*b*). The final P addition of 1.6 µmol·L^{-1} used in this study increased the DIP pool more than 10-fold and obviously saturated bacterial needs. In such a situation, phytoplankton may be responsible for a greater portion of PO_4^{3-} uptake than bacteria (Currie et al. 1986). However, some studies have shown heterotrophic bacteria in lakes to have such high requirements for P that they are not able to achieve P saturation (Vadstein et al. 1993).

Earlier radiotracer studies have revealed long turnover times for PO_4^{3-} (from 3 to >10 h) in the epilimnion of Lake Mekkojärvi, suggesting that during summer, plankton do not experience P deficiency in situ (Jones 1990; Salonen et al. 1994). This agrees with the failure of single P enrichments to noticeably increase primary production after 1 day. Rather, phytoplankton production seemed to become nutrient limited during incubation, when cellular stores run out (cf. Jones 1990). About 50% of P bound in *Daphnia* is renewed daily in Lake Mekkojärvi in the presence of the adundant *Daphnia* population (Salonen et al. 1994). Whether this could satisfy algal and bacterial needs for P is unknown. In a eutrophic lake, Nesjøvatn, in Norway, P release by the dominating zooplankton species *Daphnia galeata* usually contributed <33% of the P requirements of algae and bacteria (Vadstein et al. 1995).

Despite the fact that the energy needed for N assimilation is lowest for NH_4^+, enrichments with NH_4-N did not stimulate primary production significantly more than enrichments

© 1998 NRC Canada

with other N sources. During summer stratification of Lake Mekkojärvi, plankton production is based on nutrient regeneration (Salonen et al. 1992), which might further have explained the NH_4^+ preference of algae. Since various N treatments resulted in rather similar primary production, it was mainly the nutrient availability, not preferences, that governed N assimilation in Lake Mekkojärvi on a plankton community level.

Stimulation of photosynthetic $^{14}CO_2$ uptake following nutrient enrichment(s) has been widely used to study the nutrient limitation of phytoplankton (Dodds and Priscu 1990). The results obtained from bioassays may depend on the incubation time and the sample volume (e.g., Hecky and Kilham 1988). Gerhart and Likens (1975) stressed that one should be cautious in using small-volume enclosures in the studies of nutrient limitation, since the failure of a particular nutrient addition to stimulate production in short-term (from hours to 1–2 days) ^{14}C bioassays does not necessarily mean that this nutrient would not affect plankton growth in situ in the lake. On the other hand, long-term incubations are more susceptible to bottle effects, e.g., intensified nutrient recycling and micrograzer effects (Dodds and Priscu 1990). Our experiment consisted of incubation of small volumes of coarse-filtered water in enclosed vials for either 1 or 5 days. It is obvious that the exclusion of *Daphnia* from the vials and the prevention of vertical movements made organisms more prone to nutrient limitation than in situ, particularly in 5-day incubations, which was possibly long enough for cellular stores to run out (cf. Jones 1990). Thus, 5-day incubations may merely indicate the potential of phytoplankton production for nutrient limitation, while 1-day incubations better reflect prevailing nutrient deficiency of phytoplankton assemblages. This could explain why some nutrients failed to stimulate primary production of phytoplankton in 1-day incubations, although primary production responded positively after 5 days. It is also possible that phytoplankton responded to nutrient enrichments after a lag time of 1–2 days (cf. Hessen et al. 1994), which may be required before the response of organisms can be seen in primary productivity. Thus, our experimental design had shortcomings, but we think that the results of both 1- and 5-day incubations mainly supported each other with respect to the shifts in the nutrient limitation of phytoplankton. Further, since the observed changes in the plankton community and nutrient limitation of phytoplankton occurred rapidly after the fish introduction, we think that instead of the seasonal periodicity, the changes resulted from the fish introduction and revealed rather clear, but probably complicated, cause and effect relationships. The relatively high nutrient additions used in the bioassays, the massive fish introduction, and the special characteristics of Lake Mekkojärvi may complicate the extrapolation of the results to other natural lake ecosystems. On the other hand, the simplicity of the pelagial ecosystem of Lake Mekkojärvi rendered it possible to study effects of fish introduction with reasonable effort.

In conclusion, the potential nutrient limitation of phytoplankton production in Lake Mekkojärvi shifted from potential P limitation towards N limitation in mid-July and August. The changes in nutrient limitation appeared to be associated with biotic interactions: the introduction of whitefish and consequent trophic cascades. Thus, our results suggest that higher trophic levels can directly and indirectly modify nutrient cycling also in highly humic lakes. Because such causal relationships may be very complex, more species-specific information on plankton stoichiometry as well as uptake rates of nutrients should be obtained along with simple determinations of phytoplankton primary production. At least in small water bodies, the changes in the vertical nutrient flows and the nutrient release from the sediments should also be taken into account.

Acknowledgements

The authors wish to thank L. Arvola, U. Münster, and A. Vähätalo for their critical reading of an earlier version of the manuscript and valuable suggestions. T. Aalto kindly provided unpublished zooplankton data for Fig. 1. We thank the Lammi Biological Station of the University of Helsinki for excellent working facilities, J. Vainionpää and R. Ilola for nutrient determinations, and T. Aalto, M. Likolammi, V. Lindblom, and A. Vähätalo for their help in the field. This study was supported by the Maj and Tor Nessling Foundation, University of Helsinki, and the Academy of Finland.

References

Carpenter, S.R., Cottingham, K.L., and Schindler, D.E. 1992. Biotic feedbacks in lake phosphorus cycles. Trends Ecol. Evol. **7**: 332–336.

Currie, D.J., Bentzen, E., and Kalff, J. 1986. Does algal–bacterial phosphorus partitioning vary among lakes? A comparative study of orthophosphate uptake and alkaline phosphatase activity in freshwater. Can. J. Fish. Aquat. Sci. **43**: 311–318.

Dodds, W.K., and Priscu, J.C. 1990. A comparison of methods for assessment of nutrient deficiency of phytoplankton in a large oligotrophic lake. Can. J. Fish. Aquat. Sci. **47**: 2328–2338.

Elser, J.J., Marzolf, E.R., and Goldman, C.R. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Can. J. Fish. Aquat. Sci. **47**: 1468–1477.

Elser, J.J., Lubnow, F.S., Marzolf, E.R., Brett, M.T., Dion, G., and Goldman, C.R. 1995*a*. Factors associated with interannual and intraannual variation in nutrient limitation of phytoplankton growth in Castle Lake, California. Can. J. Fish. Aquat. Sci. **52**: 93–104.

Elser, J.J., Stabler, L.B., and Hassett, R.P. 1995*b*. Nutrient limitation of bacterial growth and rates of bacterivory in lakes and oceans: a comparative study. Aquat. Microb. Ecol. **9**: 105–110.

Gerhart, D.Z., and Likens, G.E. 1975. Enrichment experiments for determining nutrient limitation: four methods compared. Limnol. Oceanogr. **20**: 649–653.

Hecky, R.E., and Kilham, P. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnol. Oceanogr. **33**: 796–822.

Hessen, D.O., Andersen, T., and Faafeng, B. 1992. Zooplankton contribution to particulate phosphorus and nitrogen in lakes. J. Plankton Res. **14**: 937–947.

Hessen, D.O., Nygaard, K., Salonen, K., and Vähätalo, A. 1994. The effect of substrate stoichiometry on microbial activity and carbon degradation in humic lakes. Environ. Int. **20**: 67–76.

Jansson, M., Blomqvist, P., Jonsson, A., and Bergström, A.-K. 1996. Nutrient limitation of bacterioplankton, autotrophic and

© 1998 NRC Canada

mixotrophic phytoplankton, and heterotrophic nanoflagellates in Lake Örträsket. Limnol. Oceanogr. **41**: 1552–1559.

Jones, R.I. 1990. Phosphorus transformations in the epilimnion of humic lakes: biological uptake of phosphate. Freshwater Biol. **23**: 323–337.

Jones, R.I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia, **229**: 73–91.

Kankaala, P. 1988. The relative importance of algae and bacteria as food for *Daphnia longispina* (Cladocera) in a polyhumic lake. Freshwater Biol. **19**: 285–296.

Kitchell, J.F., Koonce, J.F., and Tennis, P.S. 1975. Phosphorus flux through fishes. Verh. Int. Ver. Theor. Angew. Limnol. **19**: 2478–2484.

Koroleff, F. 1983. Simultaneous oxidation of nitrogen and phosphorus compounds by persulfate. *In* Methods of seawater analysis. *Edited by* K. Grasshoff, M. Eberhardt, and K. Kremling. Verlag Chemie, Weinheimer, Germany. pp. 168–169.

Latja, R., and Salonen, K. 1978. Carbon analysis for the determination of individual biomasses of planktonic animals. Verh. Int. Ver. Limnol. **20**: 2556–2560.

Levine, S.N., and Schindler, D.W. 1992. Modification of the N:P ratio in lakes by in situ processes. Limnol. Oceanogr. **37**: 917–935.

Makarewicz, J.C., and Likens, G.E. 1979. Structure and function of the zooplankton community of Mirror Lake, New Hampshire. Ecol. Monogr. **49**: 109–127.

Münster, U., Einiö, P., Nurminen, J., and Overbeck, J. 1992. Extracellular enzymes in a polyhumic lake: important regulators in detritus processing. Hydrobiologia, **229**: 225–238.

Murphy, J., and Riley, J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta, **27**: 31–36.

Nygaard, K., and Tobiesen, A. 1993. Bacterivory in algae: a survival strategy during nutrient limitation. Limnol. Oceanogr. **38**: 273–279.

Porter, K.G., Pace, M.L., and Battey, F.J. 1979. Ciliate protozoans as links in freshwater planktonic food chains. Nature (Lond.), **227**: 563–565.

Salonen, K. 1981. Rapid and precise determination of total inorganic carbon and some gases in aqueous solutions. Water Res. **15**: 403–406.

Salonen, K., Kankaala, P., Tulonen, T., Hammar, T., James, M., Metsälä, T.-R., and Arvola, L. 1992. Planktonic food chains of a highly humic lake. II. A mesocosm experiment in summer during dominance of heterotrophic processes. Hydrobiologia, **229**: 143–157.

Salonen, K., Jones, R.I., DeHaan, H., and James, M. 1994. Radiotracer study of phosphorus uptake by plankton and redistribution in the water column of a small humic lake. Limnol. Oceanogr. **39**: 69–83.

Schelske, C.L., Stoermer, E.F., Fahnenstiel, G.L., and Haibach, M. 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. **43**: 407–415.

Schindler, D.E., Kitchell, J.F., He, X., Carpenter, S.R., Hodgson, J.R., and Cottingham, K.L. 1993. Food web structure and phosphorus cycling in lakes. Trans. Am. Fish. Soc. **122**: 756–772.

Schindler, D.W., Schmidt, R.V., and Reid, R.A. 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. J. Fish. Res. Board Can. **29**: 1627–1631.

Solórzano, L. 1969. Determination of ammonia in natural waters by the phenolhypoclorite method. Limnol. Oceanogr. **14**: 799–801.

Sterner, R.W., and Hessen, D.O. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. Annu. Rev. Ecol. Syst. **25**: 1–29.

Threlkeld, S.T. 1987. Experimental evaluation of trophic-cascade and nutrient-mediated effects of planktivorous fish on plankton community structure. *In* Predation, direct and indirect impacts on aquatic communities. *Edited by* W.C. Kerfoot and A. Sih. University Press of New England, Hanover and London. pp. 161–173.

Vadstein, O., Olsen, Y., and Reinartsen, H. 1993. The role of planktonic bacteria in phosphorus cycling in lakes — sink and link. Limnol. Oceanogr. **38**: 1539–1544.

Vadstein, O., Brekke, O., Andersen, T., and Olsen, Y. 1995. Estimation of phosphorus release rates from natural zooplankton communities feeding on planktonic algae and bacteria. Limnol. Oceanogr. **40**: 250–262.

Vanni, M.J., Layne, C.D., and Arnott, S.E. 1997. "Top-down" trophic interactions in lakes: effects of fish on nutrient dynamics. Ecology, **78**: 1–20.

Wood, E.D., Armstrong, F.A.J., and Richards, F.A. 1967. Determination of nitrate in sea water by cadmium–copper reduction to nitrite. J. Mar. Biol. Assoc. U.K. **47**: 23–31.

© 1998 NRC Canada

Effects of recent ecosystem changes on the recruitment of young-of-the-year fish in western Lake Erie

Gouthaman Gopalan, David A. Culver, Lin Wu, and Bruce K. Trauben

Abstract: We compared the variability in forage fish recruitment over the last 27 years against major ecological changes that occurred in Lake Erie over the same time period. During a period of high adult walleye abundance and declining phosphorus loading (1976–1982), we observed a decline in the abundance of later hatching forage fish species (e.g., July) and those species that did not shift their diets from zooplankton to benthos during the summer of their life. During years of high young-of-the-year (YOY) white perch abundance (1983–1990), forage fishes whose hatching dates and (or) diet overlapped with YOY white perch declined in abundance. When the zebra mussel (*Dreissena polymorpha*) became abundant (1991–1995), most forage fishes showed no change in abundances. Given a YOY's ability to switch to benthos during summer, the date on which this occurred was determined by a combination of zooplankton abundance and fish size. Hence, the dates individual taxa of fish hatch relative to seasonal cycles of zooplankton abundance and the size at which they can undergo an ontogenetic diet shift to benthos and (or) fish could be influencing fish growth and recruitment and need to be incorporated into YOY recruitment models.

Résumé : Nous avons comparé la variabilité du recrutement des poissons fourrage depuis 27 ans en regard des principales modifications écologiques survenues dans le lac Érié durant le même laps de temps. Pendant une période de forte abondance de doré jaune adulte et de baisse de la charge en phosphore (1976–1982), nous avons observé une baisse de l'abondance des espèces fourrage à éclosion tardive (p.ex. juillet) et des espèces qui ne passaient pas d'une alimentation zooplanctonique à une alimentation benthique pendant l'été. Pendant les années de forte abondance des jeunes de l'année de baret (1983–1990), les poissons fourrage dont les dates d'éclosion et/ou la nourriture recoupaient celles des jeunes barets ont accusé une baisse de l'abondance. Quand la moule zébrée (*Dreissena polymorpha*) a commencé à abonder (1991–1995), on n'a observé aucun changement de l'abondance chez la plupart des espèces fourrage. Étant donné que les jeunes de l'année peuvent passer à une alimentation benthique pendant l'été, la date d'occurrence de ce phénomène a été déterminée par une combinaison de l'abondance du zooplancton et de la taille des poissons. En conséquence, les dates d'éclosion des divers taxons de poissons par rapport aux cycles saisonniers d'abondance du zooplancton, et la taille à laquelle ils peuvent subir le passage ontogénique à l'alimentation benthique et (ou) piscivore, pourraient influer sur la croissance et le recrutement, et doivent être intégrées aux modèles du recrutement des jeunes de l'année.

[Traduit par la Rédaction]

Introduction

Lake Erie has undergone major ecological changes in the last 27 years. Phosphorus loading into the lake has been dramatically reduced with concomitant increase in the nitrogen:phosphorus (N:P) ratio (Dolan 1993). Phosphorus declines and increase in the N:P ratio led to a reduction in total phytoplankton biomass of 40% by the late 1970s and 65% by the mid-1980s in the western basin. Nuisance algal species abundance and biomass decreased by 85% by the mid-1980s (Makarewicz and Bertram 1991; Makarewicz 1993). The fish species composition has also changed during this time period. For example, adult walleye (*Stizostedion vitreum vitreum*) abundance has increased sharply since 1976 (Hatch et al. 1987). White perch (*Morone americana*) became abundant in the mid-1980s, while white bass (*Morone chrysops*) and yellow perch (*Perca flavescens*) abundances decreased (ODNR 1995). The zebra mussel (*Dreissena polymorpha*), an exotic species introduced from Europe, has increased dramatically in abundance since 1989. Increased water clarity and reduced levels of phytoplankton have been observed in the western basin of Lake Erie since abundance of zebra mussels increased (Leach 1992).

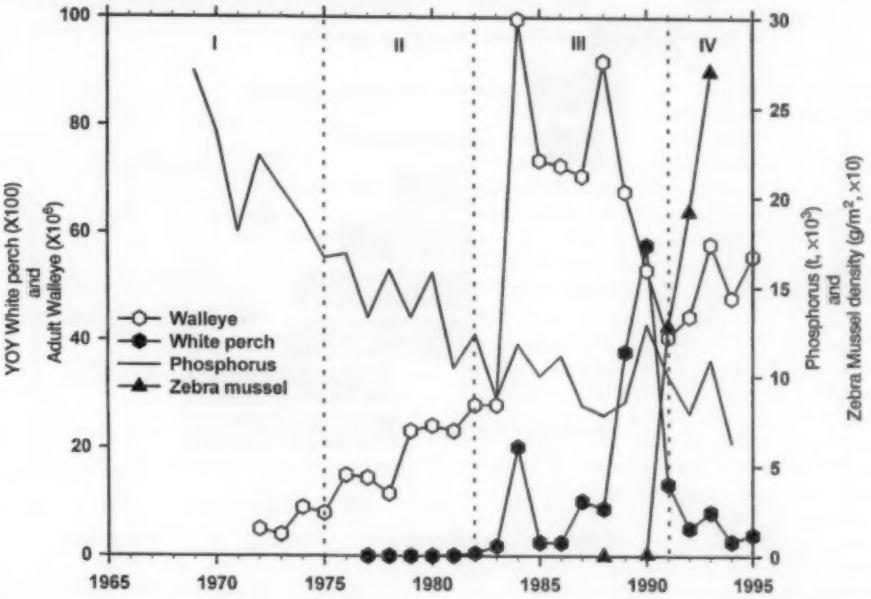
Young-of-the-year (YOY) fish contribute both to recruitment and to the food base of adult fish. The composition of Lake Erie's YOY fish community has shifted in the last 25 years with decreases in shiners (*Notropis* spp.), alewife (*Alosa pseudoharengus*), and white bass and increases in walleye and white perch populations (Knight and Vondracek 1993). Ecological changes in western Lake Erie could have contributed to changes in recruitment of YOY fishes. In de-

Received April 2, 1997. Accepted September 2, 1998.
J13944

G. Gopalan and D.A. Culver. Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, U.S.A.
L. Wu. Department of Biology, Mount Union College, 1972 Clark Avenue, Alliance, OH 44601, U.S.A.
B.K. Trauben. Jackson and Campbell, P.C., 1120 20th Street NW, Suite 300 South, Washington DC 20036, U.S.A.

© 1998 NRC Canada

Fig. 1. Variation in phosphorus loading (Dolan 1993), fishable walleye abundance (ODNR 1995), YOY white perch abundance (ODNR 1995), and zebra mussel density (R. Pontius, Ohio State University, personal communication) that defines the four periods of analysis for this paper. YOY white perch are expressed as catch per trawl hour (CPTH). Zebra mussel density expressed in dry weight of soft tissue based on samples collected at an index site at Peach Point on South Bass Island.



signing our analysis, we considered the types of biotic interactions that could occur among YOY fish and components of the western Lake Erie ecosystem. Adult walleye primarily affect YOY survival and recruitment through predation, whereas white perch compete with YOY species for zooplankton. Reduction in phosphate loading and zebra mussel grazing on algae may indirectly affect the zooplankton supply of the YOY fishes. Hence, study on the diets of YOY fishes is needed if YOY survival and recruitment are to be better understood. Ontogenetic diet shifts help the fish utilize additional and (or) alternate food resources. The ontogeny of YOY diets is affected by zooplankton abundance, fish size, and fish age (Mills and Forney 1983; Werner and Gilliam 1984; Wu and Culver 1992). Changes in zooplankton abundance are more likely to affect fishes that are unable to switch to an alternate diet. The relative synchrony of seasonal changes in zooplankton abundance and YOY fish growth could be critical to the study of YOY survival and recruitment.

In this study we combined information on zooplankton and fish abundances, diet, and growth to estimate the relative importance of (*i*) an increase in the adult walleye population, (*ii*) an increase in the white perch population, (*iii*) reduced phosphorus loading, and (*iv*) the introduction of zebra mussels on changes in YOY fish species abundance and composition in Lake Erie from 1969 to 1995.

Materials and methods

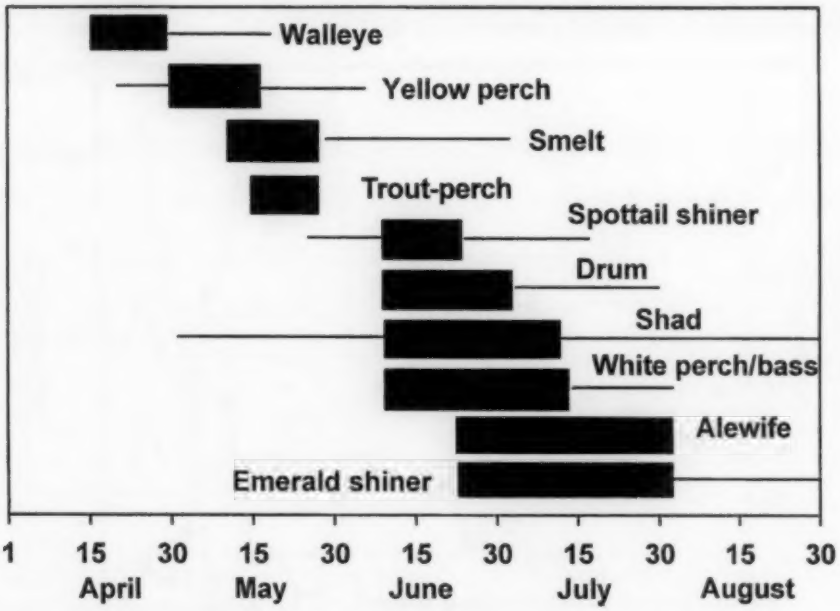
We examined Lake Erie fish data collected for four periods (Fig. 1): period I (1969–1975), low adult walleye abundance and high phosphorus loading; period II (1976–1982), high adult walleye abundance, declining phosphorus loading, and low YOY white perch abundance; period III (1983–1990), higher adult walleye abundance, low phosphorus loading, and high YOY white perch abundance; period IV (1991–1995), as in period III plus high zebra mussel abundance. For each period we characterized the forage fish abundances. The YOY fish diets were also examined for the relative contribution of zooplankton, benthos, and fish to YOY diets, diet overlaps, and stomach fullness.

We obtained annual forage fish abundance data and mean lengths of YOY white bass and YOY yellow perch during August and October for western basin of Lake Erie. The fish were collected from paired 15-min trawls done biweekly in August and October of every year from 1969 to 1995. The trawls were part of Ohio Division of Wildlife's (ODW) regular YOY recruitment monitoring cruises (Eckmayer 1988; Knight and Vondracek 1993; ODNR 1995). Details of fish trawling methods along with sampling sites are given in ODNR (1995) and Knight and Vondracek (1993). The geometric mean of the forage fish catch per trawl hour data from two offshore index stations (>9 m depth) sampled in October of each year was log transformed to approximate a normal distribution before statistical analysis. Forage fish studied were those that were vulnerable to walleye (Knight et al. 1984; Knight and Vondracek 1993). The list included YOY white bass, gizzard shad (*Dorosoma cepedianum*), alewife, white perch, yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and walleye plus all sizes of emerald shiner (*Notropis atherinoides*), spottail shiner (*Notropis hudsonius*), rainbow smelt (*Osmerus mordax*), and trout-perch (*Percopsis omiscomaycus*).

In 1983 and 1984, ODW collected YOY fish used for our diet analyses during 10-min tows with an otter (bottom) trawl (12.7-mm mesh stretched) at an inshore site 200 m from the shore and 8 m deep near Bono, Ohio, and an offshore site 25 km north of Bono and 13 m deep near Middle Sister Island. Both sites had a muddy bottom. Sampling was done at midday, except on the first and last sampling dates at the Middle Sister Island site for 1983

© 1998 NRC Canada

Fig. 2. Peak abundance of fish larvae (bars) in ichthyoplankton net samples for western basin of Lake Erie in 1975, 1976, and 1977. The lines indicate first and last day of occurrence. Data are from Heniken (1977) and Mizera et al. (1981).



and 1984, when sampling was done once every 3 h over a 24-h period. In 1984, only the offshore site was sampled. In 1988 and 1989, YOY fishes and zooplankton were sampled weekly in the western basin of Lake Erie at both nearshore (41°33′53″N, 82°47′56″W) and offshore (41°38′67″N, 82°46′44″W) locations near East Harbor, Ohio, during June through August. Depths of these sites were 6 and 10 m, respectively. Further description of the habitat along with the temperature profile, zooplankton, and fish collection methods for the 1988 and 1989 sampling are given in Wu and Culver (1992).

We sorted and counted fish by species from samples for each date and location and did stomach content analysis on 10 randomly chosen fish for YOY of each available species. We identified cladocerans and cyclopoid copepods in fish and plankton samples to the species level, and calanoid copepods and all benthic organisms to genus. Algae, protozoans, and rotifers observed in stomachs of fish (primarily gizzard shad) were not quantified. Different species of food items found in the gut of YOY fishes were further classified into three categories: "zooplankton," organisms which we found in the pelagic part of the water column; "benthos," invertebrates like ostracods, benthic copepods, benthic cladocerans, and insect larvae (e.g., chironomids) that inhabit the benthic layer; and "fish." We estimated the biomass of invertebrate species found in the gut by measuring the length of each organism and using length–mass regression equations (Dumont et al. 1975; Rosen 1981; Culver et al. 1985; S.P. Madon (Department of Biological Sciences, Pace University, Pleasantville, N.Y., personal communication)). To develop length–mass relationships for fish we measured the lengths and dry mass with the stomach removed for each sampling date after drying them at 80°C in oven for 48 h. We calculated the total mass of fish (all species combined) collected during each year to provide a measure of variation in the total YOY recruitment:

$$\text{Total mass of fish (g dry wt.)} = \sum W_i C_i$$

where W_i is average mass of YOY species i during summer, and C_i is the geometric mean of catch per trawl hour for YOY species i in each year.

We estimated the diet overlap between species for individual prey taxa using Schoener's index (Schoener 1970):

$$D_p = 1 - 0.5 \sum \left| P_{x,i} - P_{y,i} \right|$$

where D_p is the fraction of diet overlap, $P_{x,i}$ and $P_{y,i}$ are the proportion of prey species i (by mass) eaten by fish species x and fish species y, respectively. D_p values greater than 0.60 are considered biologically significant (Wallace 1981), so we scored the relative number of dates that values >0.60 occurred for each species pair. Stomach fullness was estimated using the method developed by Knight and Margraf (1982).

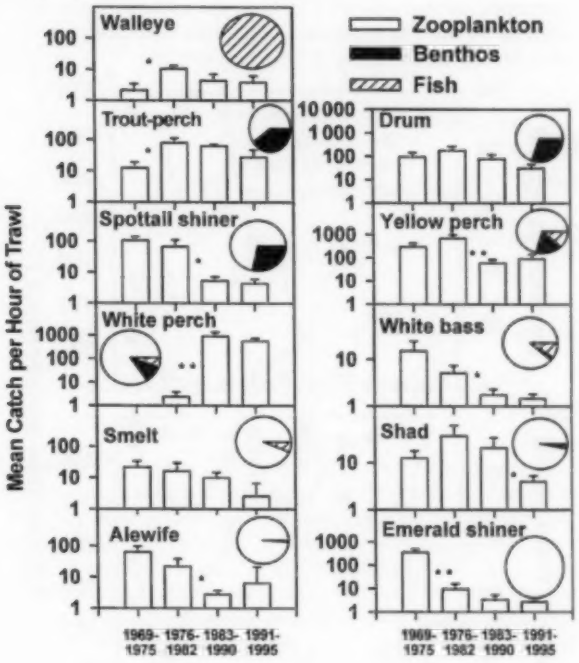
Statistical analyses for changes in forage fish abundance for each species and comparison of the fall mass of YOY white bass and YOY yellow perch were done using Student's t-test. The autocorrelation functions of the log-transformed forage fish abundance values for all species during each period were not significant; hence, the data were assumed to be independent. While comparing fish diet with forage fish abundance, we used fish diet data from 1983, 1984, and 1989. For the other years in which no diet data exist, we assumed the diet of the YOY fishes would still fall under our three broad categories: zooplankton, benthos, and fish. Agreement with other YOY dietary data available for Lake Erie (Price 1963; Wu and Culver 1992; G. Gopalan, unpublished) validates our assumption.

Results

The time of hatch varies for different fish species in western Lake Erie (Fig. 2). Predators like walleye and yellow perch hatch earliest in late spring, while planktivores like alewife and emerald shiner hatch last in midsummer. While the actual date of hatch varies from year to year, the general sequence seen here is repeated.

© 1998 NRC Canada

Fig. 3. Comparison of mean forage fish abundance (as CPTH) over four study periods and the relative contribution (by weight) of zooplankton, benthos, and fish to the diet (inset circles) of each YOY fish taxon in 1983 and 1984. See text for the definitions of the study periods. A significant difference between two adjacent bars is indicated by asterisks between them *, $p \leq 0.05$; **, $p \leq 0.01$.



Lake Erie forage fish year-class strength (YCS)

The forage fish abundance of the 11 major fish taxa varied widely among the four periods (Fig. 3). From period I (1969–1975) to period II (1976–1982), the population of emerald shiner ($p < 0.001$), YOY white bass ($p < 0.18$), and alewife ($p < 0.25$) declined, while YOY walleye ($p < 0.03$) and trout-perch ($p < 0.02$) populations increased (Fig. 3). The total forage fish abundance (in numbers) during the two periods did not differ ($p < 0.60$): period I = 1408 ± 321 catch per trawl hour (CPTH) (mean ± SE); period II = 1661 ± 330 CPTH, while biomass of forage fish (all species combined) caught per trawling hour increased from 370 ± 76 to 558 ± 101 g. While not significant ($p < 0.20$), the difference was probably biologically significant, as it occurred despite the increase in adult walleye in the lake. In period III (1983–1990), YOY white perch increased ($p < 0.001$), while all other YOY and forage fish species studied decreased in abundance (Fig. 3). Populations of YOY white bass, alewife, YOY yellow perch, and spottail shiner decreased significantly. The total number of forage fish caught (1592 ± 713 CPTH; $p < 0.91$) and total biomass of forage fish caught (507 ± 204 g; $p < 0.78$) were unchanged relative to period II. During period IV (1991–1995), when zebra mussels became abundant, only YOY gizzard shad ($p < 0.04$) and YOY drum ($p < 0.15$) decreased in abundance. The total number of forage fish caught (912 ± 235 CPTH; $p < 0.33$) and the total mass of forage fish caught (274 ± 72 g; $p < 0.16$.) also decreased.

Young-of-the-year fish diets

Zooplankton formed a major part of the late summer (July to early September) diet of all YOY fish species (Fig. 3) except YOY walleye, which fed consistently on fish. The other four taxa fed on fish at various times during summer. The YOY fishes were divided into four categories based on their diet during this sampling period (Fig. 3). Emerald shiner, alewife, and gizzard shad were categorized as eating pelagic zooplankton with little or no benthos or fish. White bass and rainbow smelt were categorized as eating zooplankton and fish with little or no benthos. White perch, yellow perch, trout-perch, freshwater drum, and spottail shiner were categorized as eating zooplankton and benthos. Walleye was categorized as eating only fish.

During period II, three of five forage species in the zooplankton or zooplankton plus fish diet categories declined in abundance relative to period I with one species declining significantly (Fig 3). Over the same period, three of five forage species in the zooplankton plus benthos diet category increased in abundance with two species increasing significantly. With the increase of white perch in period III, however, all other forage fishes declined in abundance with two of five forage species in the zooplankton or zooplankton plus fish diet categories and two of five forage species in the zooplankton plus benthos category, declining significantly.

When the dietary patterns showing the ontogenetic diet shift from zooplankton to benthos are plotted against time (Fig. 4), YOY trout-perch and YOY freshwater drum began consuming benthos earliest in the season, followed by YOY yellow perch and YOY white perch, while YOY white bass, YOY alewife, and YOY gizzard shad did not include benthos in their diet until late summer or fall. YOY emerald shiner, YOY rainbow smelt, and YOY walleye stomachs contained no benthos throughout the sampling period. In the 1989 samples, this same ontogenetic shift occurred for YOY yellow perch, YOY white perch, and YOY white bass (Fig. 5*a*). The ontogenetic diet shift occurred at low zooplankton density (50/L). Benthos formed only a minor part of YOY white bass diet compared with those of YOY yellow perch and YOY white perch. When zooplankton density increased, YOY white perch and YOY white bass started feeding on zooplankton again. During the late July low zooplankton phase, stomach fullness of YOY white bass declined the most as it did not include benthos in its diet (Fig. 5*b*). YOY white perch stomach fullness declined less, while YOY yellow perch stomach fullness did not decline at all. The body size at which YOY had 10% or more benthos in their diet differed among species (Fig. 6).

Diet overlap was biologically significant (Schoener's index ≥ 0.6 for over 50% of the sampling dates during 1983 and 1984) between YOY white perch and three other taxa (YOY white bass, YOY alewife, and YOY yellow perch) and between YOY alewife and four other taxa (YOY white bass, YOY white perch, YOY yellow perch, and YOY emerald shiner) (Fig. 7). YOY walleye diet did not overlap with species feeding on zooplankton as it had little or no zooplankton in its diet between July and September, having switched to fish much earlier. YOY rainbow smelt diet over-

© 1998 NRC Canada

Fig. 4. Seasonal variation in the importance of benthos (% of total diet by weight per fish) for YOY fish species in western basin of Lake Erie in 1983 and 1984. (*a*) Offshore site, 1984. (*b*) Offshore site, 1983. (*c*) Inshore site, 1983. WA, Walleye; TP, trout-perch; FD, freshwater drum; SS, spottail shiner; YP, yellow perch, WP, white perch; WB, white bass; RS, rainbow smelt; GS, gizzard shad; AL, alewife; ES, emerald shiner.

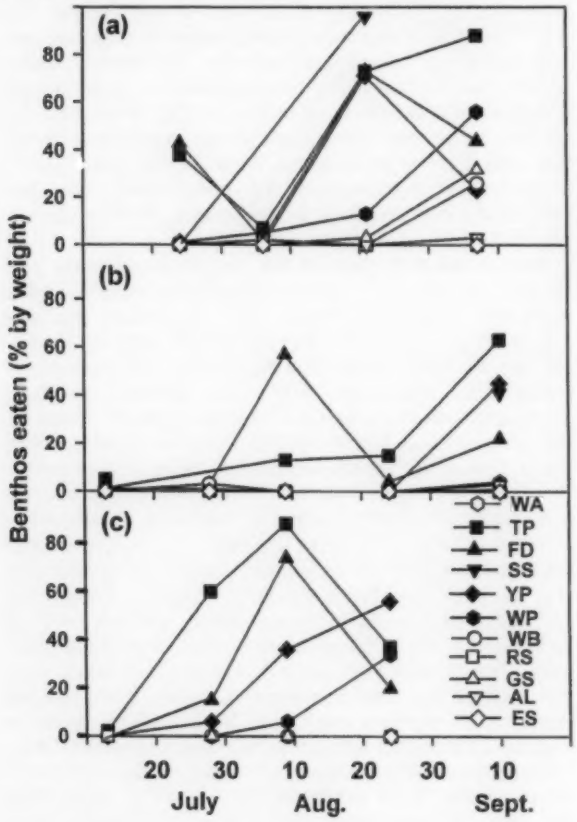
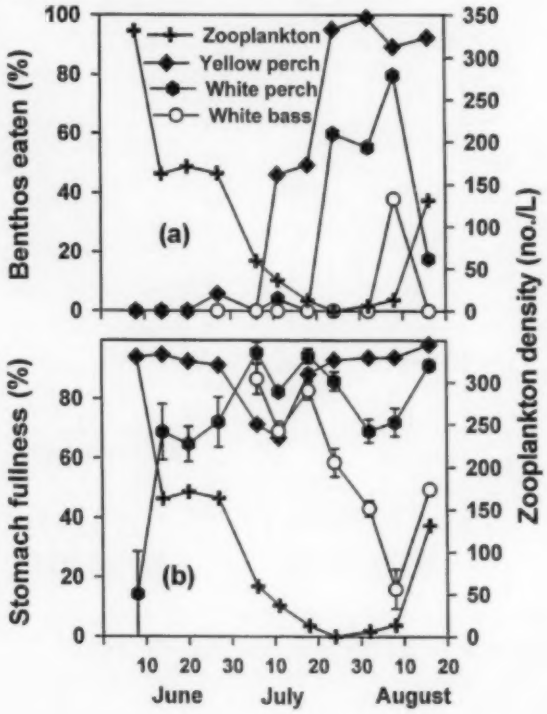


Fig. 5. (*a*) The seasonal variation in the relative contribution of benthic prey in stomach (% of total diet by weight) of YOY yellow perch, YOY white perch, and YOY white bass (left axis) compared with seasonal variation in crustacean zooplankton (cladocerans and copepods, less nauplii) abundance in the lake (right axis). $N = 10$ specimens analyzed per fish species per date. (*b*) Seasonal variation in stomach fullness (percent of maximum, left axis) for YOY of three fish species relative to seasonal variation in crustacean zooplankton abundance (right axis) for the western basin of Lake Erie in 1989.



lapped very little with the other zooplanktivores (Fig. 7) as it frequently fed on zooplankton like *Eurytemora affinis*, which did not form a major part of the diet of other YOY fish species.

The late-summer mean individual mass of YOY white bass was significantly lower for years of high white perch abundance than they were when white perch YOY was scarce (low white perch abundance: 4.49 ± 1.07 g; high white perch abundance: 0.22 ± 0.01 g). Similar results were obtained for fall mass of YOY yellow perch (low white perch abundance: 7.65 ± 0.83 g; high white perch abundance: 5.0 ± 1.06 g).

Discussion

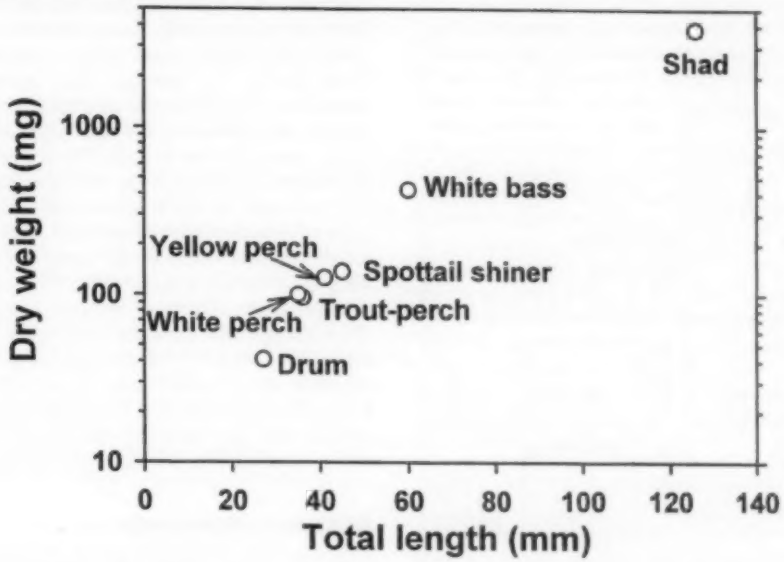
Effect of walleye predation and reduction in phosphorus loading

Gizzard shad, shiners, and smelt formed ≥ 90% of the walleye diet during 1979–1991 in the western basin (Knight et al. 1984; Francis 1992). In addition, white perch also formed an important prey item in diet of walleye in 1980s (Hartman and Margraf 1992). Nevertheless, the abundances of YOY gizzard shad, smelt, and YOY white perch either increased or were unchanged during periods II and III when walleye abundance was increasing. Only emerald shiner declined significantly during period II, while alewife and benthic-feeding spottail shiner declined later during period II and were significantly lower only in period III. YOY white bass and YOY yellow perch, which were rarely observed in walleye diet, declined significantly during period III. Hence, selective predation by increasing adult walleye population during 1970s and 1980s as proposed by Knight and Vondracek (1993) does not explain all the forage fish population changes.

YOY fish species undergo ontogenetic diet shifts as a function of zooplankton density and size (Mills and Forney 1983; Wu and Culver 1992). In addition, the minimum ontogenetic shift size to benthos (Fig. 6) varies widely among species. Fish species that hatch late or have larger ontogenetic shift size will be more reliant on zooplankton and are more likely to be affected by changes in summer zoo-

© 1998 NRC Canada

Fig. 6. Comparison of lengths and weights of seven YOY taxa at the onset of consumption of benthos (benthos ≥10% or more, by weight of total diet), data from 1983, 1984, and 1989 are combined.



plankton abundance. Three of five forage species highly reliant on zooplankton during the first summer of their lives (emerald shiner, alewife, and white bass) tended to decrease or significantly decreased in abundance during period II relative to period I. On the other hand, four of six forage species that were able to diversify their diet during the first summer because of earlier hatch or lower ontogenetic shift size (walleye, trout-perch, drum, white perch, and yellow perch) tended to increase or significantly increased during period II over period I. Reduction in phosphorus lowered algal biomass and shifted algal composition from blue-green algae to diatoms in Lake Erie (Makarewicz and Bertram 1991; Makarewicz 1993). Increase in the N:P ratio also influenced the change in algal composition (Culver 1991). Zooplankton, especially cladocerans, are negatively affected by blue-green algae (Nizan et al. 1986). Smaller algae, like diatoms and cryptomonads are more edible by zooplankton than the larger blue-green algae, resulting in greater transfer of energy from phytoplankton to zooplankton. These factors could have led to increased zooplankton productivity during period II.

Increased zooplankton productivity is more likely to occur during early summer as zooplankton densities in early summer are influenced by food abundance and, in late summer, by fish predation (Wu and Culver 1994). Therefore, fish species hatching earlier are likely to benefit more from increased zooplankton abundance in terms of higher survival and growth. In addition, improved water quality associated with reduction in phosphorus could also lead to higher survival. Fishes that hatch closer to the period of midseason zooplankton decline and are unable to diversify their diet during late summer are likely to be affected by competition from larger, early hatched species.

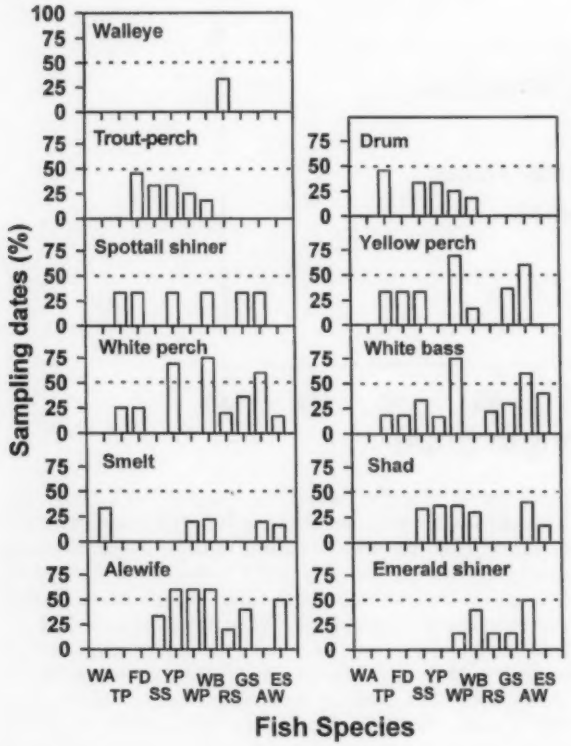
Effect of increases in white perch abundance

Zooplankton are the major food of YOY and adult white perch during summer (Parrish and Margraf 1990, 1994). The time of hatch of white perch (early June) coincides with that of many YOY species, increasing demand on zooplankton throughout the summer. The YOY fish species that depend strongly on zooplankton could suffer from reduced growth due to reduced consumption, while those species that are able to diversify to a different diet will increasingly include benthos in their diet. The growth of YOY yellow perch declines when they feed on benthos instead of zooplankton (Mills et al. 1987; Wu and Culver 1992). Reduced growth could lead to reduced recruitment by increasing the period of vulnerability to predators (Crowder et al. 1987) and by increasing overwintering mortality (Post and Evans 1989). Four species (YOY yellow perch, spottail shiner, YOY white bass, and alewife) declined significantly during the white perch increase in period III. Three of these species (YOY yellow perch, YOY white bass, and YOY alewife) also had high diet overlap with YOY white perch (Fig. 7).

YOY gizzard shad abundance did not decrease significantly from period I to periods II and III despite the fact that they had little or no benthos in their diet and were highly preferred by walleye. YOY gizzard shad undergo a different kind of ontogenetic diet shift from being a visual feeder of macrozooplankton to a pump filter feeder of microzooplankton, phytoplankton, and suspended organic matter at 25–30 mm total length (Cramer and Marzolf 1970). YOY gizzard shad can filter particles as small as 19–35 μm at 100% efficiency (Mummert and Drenner 1986). Hence these particles could play an important role in the diet of YOY gizzard shad. This filter-feeding ability combined with the ability to spawn throughout the summer (Fig. 2) could have augmented the YOY gizzard shad population during years of changes in phosphorus concentration and the abundances of walleye and white perch. YOY gizzard shad in fact increased in abundance ($p < 0.15$) during 1976–1982, when phosphorus declined, and smaller but easily digestible algae

© 1998 NRC Canada

Fig. 7. Relative frequency of dates with high dietary overlap between pairs of YOY species in western basin of Lake Erie for 1983 and 1984. Data are plotted as percent of the sampling dates on which Schoener's diet overlap index value exceeds 0.6. The broken lines indicate 50% of dates. Abbreviations are given in Fig. 4.



like diatoms and flagellates increased. Rainbow smelt was the other species with no significant population changes between adjacent time periods. This could be due to its infrequent diet overlap with other YOY species (Fig. 7) and early hatch.

Effects of increases in zebra mussel abundance

Zebra mussels did not negatively affect individual forage species, as all species except for YOY gizzard shad did not decrease significantly during period IV. Zebra mussels could still have lowered the total species abundance, because the total mass of forage fish caught decreased ($p < 0.15$) during period IV relative to period III. Zebra mussels are filter feeders on particles with little or no ability to escape like phytoplankton, dead organic suspended materials, inorganic suspended matter, protozoans, and other microzooplankton (MacIsaac et al. 1992). Many of these organisms are also filtered by YOY gizzard shad, which also depend on clay flocculation to increase consumption (Mcintyre 1983). Zebra mussels could filter and sediment these organisms and floc-forming materials and reduce gizzard shad food consumption.

Implications for the future

If zebra mussels were to reduce zooplankton levels throughout the summer, fish species hatching very early in the season with the ability to shift from a zooplankton to a benthos diet will be favored over later hatched species like shad and white perch. Later hatched species like emerald shiner and alewife might benefit from reduced food competition during late summer from gizzard shad and white perch. Gizzard shad could also be affected directly by reduction in phytoplankton and microcrustaceans. These changes could gradually lead to a shift from a gizzard shad and white perch dominated system to multispecies domination. The total abundance of YOY fishes could also decline because of reduced zooplankton abundances. Zebra mussels increase the phosphorus levels in the water column via internal recycling (Arnott and Vanni 1996). This could temporarily halt or reverse the effects of reduced phosphorus loading. The YOY recruitment for a particular year is likely to be determined by a dynamic combination of predation, the hatching schedule of individual taxa, the number and initial size of larvae, the body size and zooplankton density at which individual fish taxa undergo ontogenetic diet shifts, and the lake's zooplankton productivity during summer.

Acknowledgements

We thank the Ohio Department of Natural Resources, Ohio Division of Wildlife, for the YOY data and for letting us sample YOY fish with them in 1983–1984 and for providing extensive trawl data. This work was supported by Ohio Sea Grant Program projects (R/ER-14-PD, R/LR-1, R/ER-17-PD, R/ER-8) to D.A.C.

References

Arnott, D.L., and Vanni, M.J. 1996. Nitrogen and phosphorus recycling by zebra mussel (*Dreissena polymorpha*) in western basin of Lake Erie. Can. J. Fish. Aquat. Sci. **53**: 646–659.

Cramer, J.D., and Marzolf, G.R. 1970. Selective predation on zooplankton by gizzard shad. Trans. Am. Fish. Soc. **99**: 320–332.

Crowder, L.B., Mcdonald, M.E., and Rice, J.A. 1987. Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 141–147.

Culver, D.A. 1991. Effects of the N:P ratio in fertilizer for fish hatchery ponds. Verh. Int. Ver. Theor. Angew. Limnol. **24**: 1503–1507.

Culver, D.A., Boucherle, M.M., Bean, D.J., and Fletcher, J.W. 1985. Biomass of freshwater crustacean zooplankton from length–weight regression. Can. J. Fish. Aquat. Sci. **42**: 1380–1390.

Dolan, D. 1993. Point source loading of phosphorus to Lake Erie 1986–1990. J. Great. Lakes Res. **19**: 212–223.

Dumont, H.J., Van de Velde, I., and Dumont, S. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton, and benthos of continental waters. Oecologia, **19**: 75–97.

Eckmayer, W.J. 1988. The relationship of age, size and diet to total body lipids in young-of-the-year white bass, *Morone chrysops*. Ph.D. dissertation, Ohio State University, Columbus.

Francis, J.T. 1992. Prey selectivity by walleye in Lake Erie: an historical and inter-basin comparison. M.S. thesis, Ohio State University, Columbus.

Hartman, K.J., and Margraf, F.J. 1992. Effects of prey and predator

© 1998 NRC Canada

abundances on prey consumption and growth of walleye in western Lake Erie. Trans. Am. Fish. Soc. **121**: 245–260.

Hatch, R.W., Nepszy, S.J., Muth, K.M., and Baker, C.T. 1987. Dynamics of the recovery of the western Lake Erie walleye (*Stizostedion vitreum vitreum*) stock. Can. J. Fish. Aquat. Sci. **44**(Suppl. 2): 15–22.

Heniken, M.R. 1977. Distribution and abundance of larval fish in western Lake Erie. Center for Lake Erie Area Research, Columbus, Ohio.

Knight, R.L., and Margraf, J.F. 1982. Estimating stomach fullness in fishes. N. Am. J. Fish. Manage. **2**: 413–414.

Knight, R.L., and Vondracek, B. 1993. Changes in prey fish populations in western Lake Erie, 1969–88, as related to walleye, *Stizostedion vitreum*, predation. Can. J. Fish. Aquat. Sci. **50**: 1289–1298.

Knight, R.L., Margraf, J.F., and Carline, R.F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Trans. Am. Fish. Soc. **113**: 677–693.

Leach, J.H. 1992. Impacts of the zebra mussel, *Dreissena polymorpha*, on water quality and spawning reefs in western Lake Erie. *In* Zebra mussels: biology, impact and control. *Edited by* T. Nalepa and D. Schloesser. Lewis Publishers, Chelsea, Mich. pp. 381–397.

MacIsaac, H.J., Sprules, W.G., Johannsson, O.E., and Leach, J.H. 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Oecologia, **92**: 30–39.

Makarewicz, J.C. 1993. Phytoplankton biomass and species composition in Lake Erie 1970 to 1987. J. Great Lakes Res. **19**: 258–274.

Makarewicz, J.C., and Bertram, P. 1991. Evidence for the restoration of the Lake Erie ecosystem. Bioscience, **41**: 216–223.

Mcintyre, S.C., Jr. 1983. Flocculated algae, a potentially important food source for filter feeding fish. J. Freshwater Ecol. **2**: 193–196.

Mills, E.L., and Forney, J.L. 1983. Impact on *Daphnia pulex* of predation by young yellow perch in Oneida Lake, New York. Trans. Am. Fish. Soc. **112**: 154–161.

Mills, E.L., Forney, J.L., and Wagner, K.J. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. *In* Predation: direct and indirect impacts on aquatic communities. *Edited by* W.C. Kerfoot and A. Sih. University Press of New England, Hanover, N.H. pp. 118–131.

Mizera, J.J., Cooper, C.L., and Herdendorf, C.E. 1981. Limnetic larval fish in the nearshore zone of the western basin of Lake Erie. J. Great Lakes Res. **7**: 62–64.

Mummert, J.R., and Drenner, R.W. 1986. Effect of fish size on filtering efficiency and selective particle ingestion of a filter-feeding clupeid. Trans. Am. Fish. Soc. **115**: 522–528.

Nizan, S., Dimentman, C., and Shilo, M. 1986. Acute toxic effects of the cyanobacterium *Microcystis aeruginosa* on *Daphnia magna*. Limnol. Oceanogr. **31**: 497–502.

Ohio Department of Natural Resources (ODNR). 1995. Ohio's Lake Erie fisheries. Ohio Department of Natural Resources, Division of Wildlife, Columbus.

Parrish, D.L., and Margraf, J.F. 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined from feeding and growth. Can. J. Fish. Aquat. Sci. **47**: 1779–1787.

Parrish, D.L., and Margraf, J.F. 1994. Spatial and temporal patterns of food use by white perch and yellow perch in Lake Erie. J. Freshwater Ecol. **9**: 29–35.

Post, J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. **46**: 1958–1968.

Price, J.W. 1963. A study of food habits of some Lake Erie fish. Bull. Ohio Biol. Surv. **2**: 1–89.

Rosen, R.A. 1981. Length–weight relationships of some freshwater zooplankton. J. Freshwater Ecol. **1**: 225–229.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology, **51**: 408–418.

Wallace, R.K., Jr. 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. **110**: 72–76.

Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. **15**: 393–425.

Wu, L., and Culver, D.A. 1992. Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): a size-related response to zooplankton density. Can. J. Fish. Aquat. Sci. **49**: 1932–1937.

Wu, L., and Culver, D.A. 1994. *Daphnia* population dynamics in western Lake Erie: regulation by food limitation and yellow perch predation. J. Great. Lakes. Res. **20**: 537–545.

© 1998 NRC Canada

Estimators of stream residence time of Pacific salmon (*Oncorhynchus* spp.) based on release–recapture data

James M. Lady and John R. Skalski

Abstract: The area-under-the-curve method is a widely used method for estimating salmon escapement. The method depends on obtaining an accurate estimate of stream residence time, or stream life. This paper develops two estimators of stream residence time based on release–recapture data: a nonparametric estimator and a parametric estimator. Monte Carlo simulations showed that with an adequate release size and number of sampling occasions, both estimators provide precise estimates of stream residence time. If there is significant right censoring, however, the parametric estimator is significantly less biased. If the data are too sparse, the parametric estimator performs poorly and often fails. The stream residence time of spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska, was estimated using the estimators developed here. Because the estimators also provide the variance of the estimates, the precision of the stream residence time estimate could be assessed, and we were able to test and reject the hypothesis that the stream residence time for females is equal to that of males. Both estimators are applicable to estimating the life expectancy of any fish or wildlife population with release–recapture techniques.

Résumé : La méthode de l'aire sous la courbe est largement utilisée pour estimer l'échappée des saumons. Pour être efficace, cette méthode exige qu'on dispose d'une estimation précise du temps de séjour des poissons dans le cours d'eau. On présente dans cet article deux estimateurs du temps de séjour en cours d'eau fondés sur des données de lâcher et de recapture, soit un estimateur non paramétrique et un estimateur paramétrique. Les simulations de Monte Carlo ont montré que si on lâche un nombre adéquat d'individus et qu'on dispose d'un nombre adéquat d'occasions d'échantillonnage, les deux estimateurs donnent des estimations précises du temps de séjour. S'il y a censuration à droite appréciable, cependant, l'estimateur paramétrique est significativement moins biaisé. Si les données sont trop peu abondantes, l'estimateur paramétrique ne donne que des résultats médiocres ou nuls. Le temps de séjour en cours d'eau du saumon rouge (*Oncorhynchus nerka*) reproducteur du lac Iliamna, en Alaska, a été estimé au moyen des estimateurs présentés ici. Comme les estimateurs fournissent aussi la variance des estimations, la précision de l'estimation du temps de séjour en cours d'eau a pu être évaluée, et nous avons pu tester puis rejeter l'hypothèse suivant laquelle le temps de séjour des femelles est égal à celui des mâles. Les deux estimateurs peuvent être utilisés pour estimer l'espérance de vie de toute population de poissons ou d'autres espèces fauniques avec des techniques de lâcher et de recapture.

[Traduit par la Rédaction]

Introduction

The uncertainty around the status of Pacific salmon (*Oncorhynchus* spp.) has increased awareness among fisheries managers of the importance of obtaining accurate estimates of escapement in order to assess the health of salmon stocks. One widely used method for estimating escapement is the area-under-the-curve method in which escapement is defined as the total number of fish-days divided by the stream residence time. Stream residence time is defined as the number of days that the average spawner is alive in the spawning area and is also referred to in the literature as "survey life" or "stream life." Past studies have focused on estimating the total number of fish-days and have used some fixed predetermined value for stream residence time (Beidler and Nickelson 1980; Ames 1984). However, more recent research has found that extrapolating estimates of stream residence time across years and across streams may potentially introduce serious bias in the estimate of escapement; estimates of stream residence time should be site specific and time specific (Perrin and Irvine 1990).

Perrin and Irvine (1990) summarized eight existing estimators of stream residence time. Liao (1994) evaluated two of these estimators: (*i*) the number of days between peak live and peak dead counts and (*ii*) the number of days between equivalence points on the cumulative live and dead count curves. He found them to be ill-defined and to have "systematic and substantial" bias. None of the estimators are statistically valid, and all have been found to be biased (English et al. 1992).

The objectives of this paper are to (*i*) develop statistically valid estimators of stream residence time based on release–recapture data, (*ii*) evaluate the performance of the estima-

Received January 15, 1998. Accepted August 22, 1998.
J14399

J.M. Lady[1] **and J.R. Skalski.** School of Fisheries, University of Washington, Seattle, WA 98101-2509, U.S.A.

[1]Author to whom all correspondence should be addressed.
e-mail: jiml@cqs.washington.edu

© 1998 NRC Canada

tors, and (*iii*) apply the estimators to a population of Iliamna Lake, Alaska, sockeye salmon (*Oncorhynchus nerka*) described in the next section. Two estimators will be developed. The first is a nonparametric estimator based on existing estimates of survival from one sampling event to the next (Cormack 1964; Burnham et al. 1987). The second estimator is a parametric estimator that assumes a probability model for the stream survival process. For both estimators, it is assumed that the marked fish are a random sample of the fish entering the spawning area at the same time. No inference is made to fish entering earlier or later than the marked fish; fish entering the spawning area at a different time may have a different expected stream residence time.

The estimators of stream residence time have a more general application to estimating the life expectancy of any fish or wildlife populations using release–recapture data. Release–recapture models have traditionally focused on the estimation of survival from one event to the next, but very little has been done on estimating the expected life expectancy of individuals in the population outside the context of life table analyses.

Example of stream residence time for sockeye salmon

Quinn and Foote (1994) studied the effects of body size and sexual dimorphism on the reproductive behavior of sockeye salmon in Iliamna Lake. The sockeye salmon were tagged at a beach in Iliamna Lake. The details of the study are given in Quinn and Foote (1994). The present paper will use the data from their study to estimate stream residence time. Although the individuals in this example were not in a stream, estimators of stream residence time can still be used to estimate the average life expectancy of the individuals. The gender of each tagged individual was recorded, so the stream residence time of each sex can be estimated and statistical inferences can be made regarding the differences in stream residence time between males and females.

There were 183 fish that were determined to be resident spawners in the study area, consisting of 101 males and 82 females. At the beginning of the study, each fish was given a unique identifying tag and released. The study area was surveyed once a day for the first 2 days and twice a day thereafter until no more tagged fish were detected. On each survey, data related to spawning behavior were recorded for each tagged fish encountered. For this paper, each day was considered a sampling occasion. If an individual was detected on at least one survey of a given day, it was considered detected on that sampling occasion. No males were detected on the final sampling occasion, resulting in a total of 12 sampling occasions for the males and 13 for the females.

It should be noted that the resulting estimates of stream residence time from these data may not reflect the true stream residence time for the population because the fish were not tagged as they entered the spawning area, but instead were captured with a beach seine and then tagged. However, great care was taken to ensure that the females included in the study had not spawned and that the males were not scarred. Also, the tagging took place within the first 2 or 3 days of the beginning of the spawning season (Quinn and Foote 1994).

Estimators of stream residence time

Nonparametric estimator

Cormack (1964) developed an estimator of the conditional survival probabilities from one occasion to the next based on release–recapture data. Burnham et al. (1987) presented a special case of the Cormack model in which individuals are tagged and released only on the initial sampling occasion. This special case of the Cormack model is the starting point for developing a nonparametric estimator of stream residence time. The estimates of the survival probabilities are derived using maximum likelihood estimation.

For a study with K sampling occasions, the parameters to be estimated are S_i, the probability that an individual alive at sampling occasion i will be alive at sampling occasion $i + 1$ (for $i = 1,..., K - 2$); P_i, the probability that an individual alive at sampling occasion i will be detected at sampling occasion i (for $i = 2,..., K - 1$); and λ, the product $S_{K-1}P_K$ (the final survival probability and detection probability are not separately estimable). The resulting likelihood function is as follows:

$$L(\underset{\sim}{S}, \underset{\sim}{P}, \lambda \mid \underset{\sim}{a}, \underset{\sim}{c}) \propto \left(\prod_{i=1}^{K-2} S_i^{v_i}\right)\left(\prod_{i=2}^{K-1} P_i^{a_i}(1-P_i)^{v_{i-1}-a_i}\right) \times \left(\prod_{i=1}^{K-1} \chi_i^{c_i}\right)\lambda^{v_{K-1}}$$

where a_i is the number of marked individuals detected at sampling occasion i, c_i is the number of marked individuals detected for the last time at sampling occasion i, v_i is the number of marked individuals known to be alive at sampling occasion $i + 1$, given by

$$v_i = R - \sum_{j=1}^{i} c_j,$$

R is the number of individuals tagged at the initial sampling occasion, and χ_i is the probability that an individual alive at occasion i will not be detected after occasion i. The maximum likelihood estimators for the survival parameters, along with estimators of their variances and covariances, are equivalent to the Burnham et al. (1987) estimates and are as follows:

$$\hat{S}_1 = \frac{a_2 v_2}{R(a_2 - c_2)}$$

$$\hat{S}_i = \frac{a_{i+1}(a_i - c_i)v_{i+1}}{a_i v_i (a_{i+1} - c_{i+1})} \quad \text{for } i = 2,..., K-2$$

$$\widehat{\mathrm{Var}}(\hat{S}_1 \mid S_1) = \frac{\hat{S}_1}{R}\left(\frac{\hat{\chi}_2(1-\hat{P}_2)^2}{(1-\hat{\chi}_2)\hat{P}_2} + \frac{\hat{\chi}_2^2\hat{P}_2(1-\hat{P}_2)\hat{S}_1}{(1-\hat{\chi}_1)(1-\hat{\chi}_2)} + \frac{\hat{\chi}_1 S_1}{(1-\hat{\chi}_1)}\right)$$

© 1998 NRC Canada

$$\hat{\mathrm{Var}}(\hat{S}_i \mid S_i) = \frac{\hat{\chi}_{i+1}(1-\hat{P}_{i+1})^2\hat{S}_i^2}{(1-\hat{\chi}_{i+1})\hat{E}(a_{i+1})} + \frac{\hat{\chi}_{i+1}^2\hat{P}_{i+1}^2(1-\hat{P}_{i+1})\hat{S}_i^3}{(1-\hat{\chi}_i)(1-\hat{\chi}_{i+1})\hat{E}(a_{i+1})} + \frac{\hat{\chi}_i\hat{S}_i^2}{(1-\hat{\chi}_i)\hat{E}(a_i)} \quad \text{for } i = 2,\ldots, K-2$$

where

$$\hat{E}(a_i) = R\left(\prod_{j=1}^{i-1}\hat{S}_j\right)\hat{P}_i$$

$$\hat{P}_2 = \frac{a_2}{R\hat{S}_1}$$

$$\hat{P}_i = \frac{a_i(a_{i-1}-c_{i-1})}{a_{i-1}v_{i-1}\hat{S}_{i-1}} \quad \text{for } i = 2,\ldots, K-1$$

$$\hat{\chi}_1 = \frac{c_1}{R}$$

$$\hat{\chi}_i = \frac{c_i}{a_i} \quad \text{for } i = 1,\ldots, K-1$$

where $\hat{E}(a_i)$ is the estimate of the expected number detected at occasion i. The corresponding estimates of the covariances are

$$\hat{\mathrm{Covar}}(\hat{S}_i, \hat{S}_{i+1}) = -\frac{\hat{S}_i\hat{S}_{i+1}\hat{\chi}_{i+1}(1-\hat{P}_{i+1})}{(1-\hat{\chi}_{i+1})\hat{E}(a_{i+1})} \quad \text{for } i = 1,\ldots, K-3$$

$$\hat{\mathrm{Covar}}(\hat{S}_i, \hat{S}_j) = 0 \quad \text{for } |i-j| > 1.$$

To develop an estimator of stream residence time from the estimates of the survival probabilities, two assumptions must be made: (A1) all deaths that occur in a given period between two sampling occasions occur at the midpoint of the period (or equivalently, the distribution of deaths is uniform between two sampling occasions) and (A2) all individuals alive at the penultimate sampling occasion die before the final sampling occasion. Violations of these assumptions have the potential of introducing bias into the estimate of stream residence time.

If T_k is a random variable representing the lifetime of the kth individual after entering the study area, then the stream residence time (T) is defined as the expected value of T_k:

$$T = E(T_k)$$

and an estimator of stream residence time ($\hat{T}$) can be defined as a function of the estimates of the survival probabilities ($\hat{S}_i$) as follows:

$$\hat{T} = \sum_{\text{all periods}} P(\text{death in period})E(\text{time of death in period} \mid \text{death occurred in period})$$

$$= \sum_{\text{all periods}} P(\text{death in period})(\text{midpoint of period})$$

$$= \sum_{\text{all periods}} P(\text{death in period})\left(\frac{t_i + t_{i+1}}{2}\right)$$

$$(1) \quad \hat{T} = \frac{1}{2}\sum_{i=1}^{K-2}\left\{(t_i + t_{i+1})(1-\hat{S}_i)\prod_{j=1}^{i-1}\hat{S}_j\right\} + \frac{1}{2}(t_{K-1} + t_K)\prod_{j=1}^{K-2}\hat{S}_j$$

where t_i is the time of the ith sampling occasion relative to the initial sampling occasion, $t_1 = 0$, and K is the number of sampling occasions.

To calculate the variance of $\hat{T}$, it is convenient to rewrite it as follows:

$$\hat{T} = \frac{1}{2}\underset{\sim}{\tau}'\underset{\sim}{\delta}$$

where

$$\underset{\sim}{\tau}' = [t_1 + t_2 \quad t_2 + t_3 \quad \ldots \quad t_{K-1} + t_K]$$

$$\underset{\sim}{\delta}' = [\delta_1\ \delta_2\ \ldots\ \delta_{K-2}\ \delta_{K-1}]$$

$$\delta_1 = 1 - \hat{S}_1$$

$$\delta_2 = (1-\hat{S}_2)\hat{S}_1$$

$$\delta_{K-2} = (1-\hat{S}_{K-2})\prod_{i=1}^{K-3}\hat{S}_i$$

$$\delta_{K-1} = \prod_{i=1}^{K-2}\hat{S}_i.$$

The variance of the stream residence time estimator can now be written as

$$\hat{\mathrm{Var}}(\hat{T}) = \hat{\mathrm{Var}}\left(\frac{1}{2}\underset{\sim}{\tau}'\underset{\sim}{\delta}\right) = \frac{1}{4}\underset{\sim}{\tau}'\hat{\mathrm{Var}}(\underset{\sim}{\delta})\underset{\sim}{\tau}$$

where the elements of the variance–covariance matrix $\hat{\mathrm{Var}}(\underset{\sim}{\delta})$ are calculated using the delta method as follows:

$$\hat{\mathrm{Covar}}(\delta_i, \delta_j) = \sum_{n=1}^{m}\sum_{r=1}^{m}\left(\frac{\partial\delta_i}{\partial\hat{S}_n}\right)\left(\frac{\partial\delta_j}{\partial\hat{S}_r}\right)\hat{\mathrm{Covar}}(\hat{S}_n, \hat{S}_r)$$

for $i = 1,\ldots, K-1$ and $j = 1,\ldots, K-1$. The problem is now reduced to the partial derivatives

$$\frac{\partial\delta_i}{\partial\hat{S}_j} = 0 \quad \text{for } j > i$$

$$\frac{\partial\delta_i}{\partial\hat{S}_i} = -\prod_{j=1}^{i-1}\hat{S}_j \quad \text{for } i = 1,\ldots, K-2$$

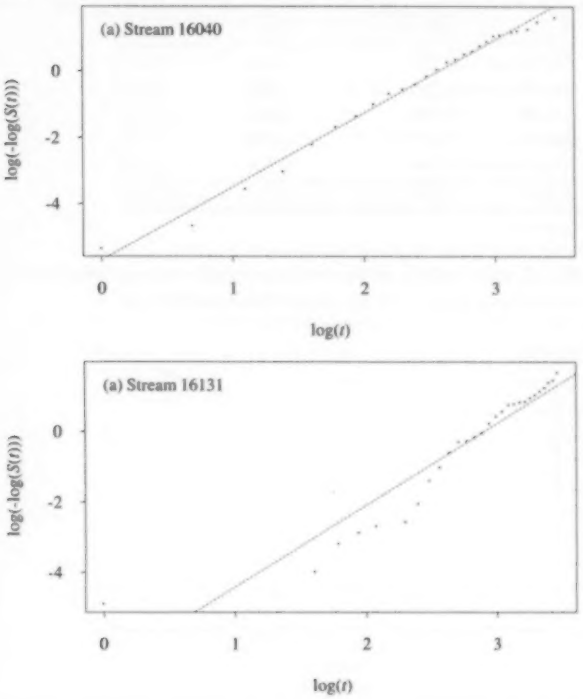
$$\frac{\partial\delta_i}{\partial\hat{S}_j} = (1-\hat{S}_i)\left(\prod_{n=1}^{j-1}\hat{S}_n\right)\left(\prod_{r=j+1}^{i-1}\hat{S}_r\right) \quad \text{for } i = 1,\ldots, K-2 \text{ and } j < i$$

$$\frac{\partial\delta_{K-1}}{\partial\hat{S}_i} = \left(\prod_{j=1}^{i-1}\hat{S}_j\right)\left(\prod_{j=i+1}^{K-2}\hat{S}_j\right) \quad \text{for } i = 1,\ldots, K-2$$

where $\prod_{i=a}^{b} f = 1$ for $a > b$ and any function f.

© 1998 NRC Canada

Fig. 1. Log–log plots of empirical survival functions for spawning pink salmon in Prince William Sound, Alaska, along with the optimal least squares lines. (*a*) Stream 16040; (*b*) stream 16131.



Parametric estimator using the Weibull distribution

An alternative to the nonparametric estimate of stream residence time is to assume a parametric model for the survival process of the spawning salmon. This allows survival to be modeled on a continuous time scale, and hence the removal of assumptions A1 and A2 above, but requires the new assumption that the survival process of the spawning salmon follow the chosen parametric model. An additional advantage of the parametric estimator is that there are fewer parameters to estimate; only the parameters of the distribution need to be estimated instead of the $K - 2$ survival probabilities.

The Weibull distribution was chosen to model the survival process of spawning salmon because (*i*) it has a closed form of the survival function and (*ii*) the hazard function for the Weibull distribution increases with time if the shape parameter is greater than 1. Also, the Weibull distribution is one of the most widely used probability distributions for modeling survival (Lawless 1982). Crosbie and Manly (1985) used the Weibull distribution with release–recapture data to model survival in an open population study.

The survival function, denoted $S(t)$, is the probability of an individual surviving up to a given time t. That is, for a random variable T:

$$(2) \qquad S(t) = P(T > t) = \exp(-(\alpha t)^{\beta})$$

where α and β are the scale and shape parameter, respectively.

The nonparametric survival probabilities (S_i) can be reparameterized using the survival function as follows:

$$(3) \qquad S_i = P(T > t_{i+1} \mid T > t_i) = \frac{P(T > t_{i+1})}{P(T > t_i)} = \frac{S(t_{i+1})}{S(t_i)} = \exp(-\alpha^{\beta}(t_{i+1}^{\beta} - t_i^{\beta})).$$

The hazard function is defined as the instantaneous rate of death at time t, given that an individual has survived up to time t. A hazard function that increases with time ($\beta > 1$) seems appropriate for a spawning population destined to die after breeding.

In order to develop a parametric estimator of stream residence time based on the Weibull distribution, the survival probabilities (S_i) are reparameterized using the survival function for the Weibull distribution (eq. 3), and the likelihood equation for a study with K sampling occasions is as follows:

$$(4) \qquad L(\alpha, \beta, \underset{\sim}{P} \mid \underset{\sim}{a}, \underset{\sim}{c}) \propto \left(\prod_{i=2}^{K-1} P_i^{a_i} (1 - P_i)^{\nu_{i-1} - a_i} \cdot \exp(-c_i (\alpha t_i)^{\beta}) \right) \times \left(\prod_{i=1}^{K-1} \chi_{(W)i}^{c_i} \right) \cdot P_K^{\nu_{K-1}} \cdot \exp(-\nu_{K-1} (\alpha t_K)^{\beta}).$$

Unlike the likelihood function for the nonparametric estimator, there are no closed-form estimates of the parameters (α, β, $\underset{\sim}{P}$), and the parameters must be estimated using numerical, iterative procedures.

The mean of the two-parameter Weibull distribution is

$$\mu = \frac{1}{\alpha} \Gamma\left(1 + \frac{1}{\beta}\right)$$

and a parametric estimate of stream residence time ($\hat{T}_P$) is as follows:

$$(5) \qquad \hat{T}_P = \frac{1}{\hat{\alpha}} \Gamma\left(1 + \frac{1}{\hat{\beta}}\right)$$

The variance of $\hat{T}_P$ can be calculated using the delta method:

$$\widehat{\mathrm{Var}}(\hat{T}_P) = \widehat{\mathrm{Var}}(\hat{\alpha}) \left(\frac{\partial \hat{T}_P}{\partial \hat{\alpha}} \right)^2 + \widehat{\mathrm{Var}}(\hat{\beta}) \left(\frac{\partial \hat{T}_P}{\partial \hat{\beta}} \right)^2 + 2\widehat{\mathrm{Covar}}(\hat{\alpha}, \hat{\beta}) \left(\frac{\partial \hat{T}_P}{\partial \hat{\alpha}} \right) \left(\frac{\partial \hat{T}_P}{\partial \hat{\beta}} \right)$$

where

$$\frac{\partial \hat{T}_P}{\partial \hat{\alpha}} = \frac{1}{\hat{\alpha}^2} \Gamma\left(1 + \frac{1}{\hat{\beta}}\right)$$

© 1998 NRC Canada

Table 1. Monte Carlo simulation results comparing two estimators of stream residence time with parameter values $R = 400$, $P(T > t_K) = 0.05$, $K = 9$, $I = 2.5$, and $P = 0.9$ using three different lifetime distributions: two empirical distributions from spawning sockeye salmon in Iliamna Lake, Alaska (Quinn and Foote 1994), and a gamma distribution.

Distribution	$\bar{T}$	Estimator	$\bar{\hat{T}}$	$\overline{\widehat{SE}(\hat{T}\mid T)}$	$\overline{\sqrt{s^2}}$	$\overline{bias}$
Stream 16040	11.26	Nonparametric	10.94	0.255	0.252	–0.314
		Parametric	11.19	0.289	0.289	–0.070
Stream 16131	15.92	Nonparametric	15.84	0.306	0.302	–0.085
		Parametric	16.05	0.327[a]	0.320	0.132
Gamma(2.5, 6)	15.00	Nonparametric	14.68	0.298	0.296	–0.326
		Parametric	14.90	0.324	0.319	–0.106

[a]Omits one iteration out of 10 000 with a negative delta method variance.

$$\frac{\partial \hat{T}_P}{\partial \beta} = \frac{1}{\hat{\alpha}}\left(\frac{\partial}{\partial \beta}\int_0^\infty t^{\frac{1}{\beta}} e^{-t} dt\right) = \frac{1}{\hat{\alpha}}\int_0^\infty \frac{\partial}{\partial \beta} t^{\frac{1}{\beta}} e^{-t} dt$$

$$= -\frac{1}{\hat{\alpha}\hat{\beta}^2}\int_0^\infty t^{\frac{1}{\beta}} (\log(t))\, e^{-t} dt.$$

The integral in the above equation has no closed-form solution, but can be evaluated numerically using Romberg integration (Press et al. 1992).

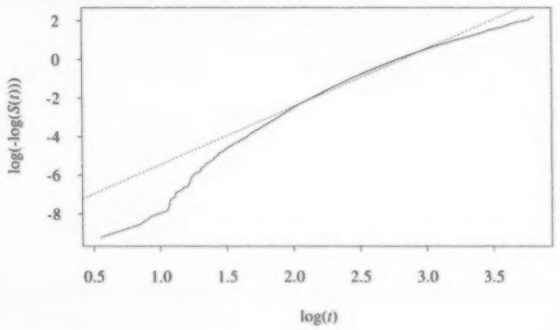
The survival function for the Weibull distribution (eq. 2) provides a way of checking how well the Weibull distribution fits data from a given study. A log–log transformation of the survival function results in a function that is linear with respect to $\log(t)$. The log–log of the empirical survival function can therefore be plotted as a function of $\log(t)$, and the degree of linearity gives a rough idea as to how well a Weibull distribution fits the data. This has been done for two streams from a study of pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska (Maki et al. 1995). The results are shown in Fig. 1, which illustrates another reason for using the Weibull distribution to model survival: there is evidence that it may be a good model for the survival process of spawning Pacific salmon.

Monte Carlo assessment of the estimators

The two estimators of stream residence time, the nonparametric estimator and the parametric estimator, were analyzed using Monte Carlo simulations. The simulations were designed to examine three issues: (*i*) the robustness of the parametric estimator to a survival process that does not follow a Weibull distribution, (*ii*) how both estimators are affected by varying amounts of right censoring, and (*iii*) how the estimators perform with varying degrees of data sparseness.

Robustness was analyzed by generating individual lifetimes from three different distributions (Table 1). The first two are the empirical distributions based on actual stream residence time data in two streams from the pink salmon study in Prince William Sound (Maki et al. 1995). The plots of the log–log transformation of the empirical survival functions (Fig. 1) indicate that both fit a Weibull distribution well, the first (stream 16040) more so than the second (stream 16131). The third distribution is a gamma(2.5, 6), chosen as a distribution that deviates significantly from a Weibull distribution (Fig. 2). All remaining simulations (Tables 2 and 3) are based on the empirical distribution for stream 16040.

Fig. 2. Log–log plot of the survival function for a gamma(2.5,6) distribution, along with the optimal least squares line.



Monte Carlo simulation procedure

Each simulation involved the selection of a sample of R individuals from the population of size $N = 40\,000$. The R individuals were selected from a finite population because the stream residence time is defined as a mean of a finite population; making inferences with respect to a finite population introduces bias in both the estimates and the variance of the estimates that is not present when making inferences with respect to an infinite population (Lady 1996). Simulations performed in Lady (1996) indicated that the ratio of the sample size to the population size had no appreciable impact on the performance of the estimators.

For each simulation, the release–recapture process was simulated on the R individuals and the stream residence time was estimated using both the nonparametric and parametric estimators. This was repeated on 500 samples of R individuals from each population, and 20 populations were generated for each simulation. The control parameters of the simulations were as follows: R, the release size, or sample size; $P(T > t_K)$, the proportion of individuals expected to be alive at the time of the last sampling occasion, or the level of right censoring; K, the number of sampling occasions; I, the time between each sampling occasion; and P, the probability of detection at each sampling occasion other than the initial occasion.

© 1998 NRC Canada

Table 2. Monte Carlo simulation results comparing two estimators of stream residence time with parameter values $R = 400$, $I = 2.5$, and $P = 0.9$ using three levels of right censoring and the empirical distribution from spawning sockeye salmon in Iliamna Lake, Alaska (Quinn and Foote 1994), for stream 16040.

$P(T > t_K)$	K	$\bar{T}$	Estimator	$\bar{\hat{T}}$	$\overline{(\hat{SE}(\hat{T}\|T))}$	$\overline{\sqrt{s^2}}$	$\overline{\text{bias}}$
0.05	9	11.25	Nonparametric	10.93	0.255	0.254	–0.316
			Parametric	11.18	0.289	0.290	–0.075
0.13	8	11.25	Nonparametric	10.60	0.229	0.226	–0.649
			Parametric	11.15	0.300[a]	0.298	–0.108
0.27	7	11.27	Nonparametric	10.05	0.197	0.195	–1.219
			Parametric	11.13	0.359	0.359	–0.139

[a]Omits three iterations out of 10 000 with a negative delta method variance.

Table 3. Monte Carlo simulation results comparing two estimators of stream residence time with parameter value $P(T > t_K) = 0.05$ using three levels of data sparseness and the empirical distribution for spawning sockeye salmon in Iliamna Lake, Alaska.

R	I	K	P	$\bar{T}$	Estimator	$\bar{\hat{T}}$	$\overline{(\hat{SE}(\hat{T}\|T))}$	$\overline{\sqrt{s^2}}$	$\overline{\text{bias}}$
400	2.5	9	0.9	11.26	Nonparametric	10.93	0.244	0.245	–0.321
					Parametric	11.19	0.278	0.280	–0.065
200	5.0	5	0.5	11.26	Nonparametric	11.00	1.092	0.870	–0.257
					Parametric	—	—	—	—
400	2.5	9	0.5	11.25	Nonparametric	10.94	0.362	0.342	–0.310
					Parametric	11.19	0.382[a]	0.384	–0.064
400	2.5	9	0.3	11.26	Nonparametric	10.73	0.607	0.561	–0.525
					Parametric	11.27	0.702[b]	0.725	0.013
1000	2.5	9	0.3	11.26	Nonparametric	10.93	0.389	0.370	0.332
					Parametric	11.23	0.415[b]	0.417	–0.030

Note: Dashes indicate that the numerical methods failed to obtain parameter estimates.
[a]Omits 18 iterations out of 10 000 with a negative delta method variance.
[b]Omits three iterations out of 10 000 with a negative delta method variance.

Table 4. Release–recapture statistics for spawning sockeye salmon in Iliamna Lake, Alaska (Quinn and Foote 1994).

Day (sampling occasion)	Number detected (a_i)			Number detected for the last time (c_i)		
	Males	Females	Total	Males	Females	Total
1	101	82	183	0	0	0
2	67	71	138	0	0	0
3	56	49	105	1	0	1
4	86	80	166	8	1	9
5	73	74	147	3	3	6
6	72	78	150	7	3	10
7	75	75	150	18	10	28
8	58	64	122	24	11	35
9	40	54	94	19	17	36
10	21	37	58	13	15	28
11	8	22	30	7	16	23
12	—	6	6	—	3	3

The following were calculated for the $s = 500$ samples from each population for each of the two estimators: T, the actual stream residence time for the population of N individuals; $\bar{\hat{T}}$, the mean of the estimates of stream residence time; $\overline{(\hat{SE}(\hat{T}|T))} = \overline{\hat{Var}(\hat{T}|T)}^{1/2}$, the mean delta method standard error; $\sqrt{s^2}$, the sample standard error, given by

$$\left(\sum_s \frac{(\hat{T}_i - \bar{\hat{T}})^2}{S-1}\right)^{1/2},$$

a measure of the true variance; and $\bar{\hat{T}} - T$, the bias. The mean of the above statistics were calculated across the 20 populations and the results are reported in Tables 1–3.

Monte Carlo simulation results

The simulation results in Tables 1–3 show that both the nonparametric estimator and the parametric estimator are capable of providing precise estimates of stream residence time. The nonparametric estimator generally had a smaller variance, and the parametric estimator generally was less biased. The larger variance of the parametric estimator was presumably due to the $1/\hat{\alpha}$ term in the parametric estimator of stream residence time. For small values of α, small variations in $\hat{\alpha}$ will result in a large change in the resulting estimate of stream residence time. The larger bias for the nonparametric estimator is due to the assumptions that all deaths in a period occur at the midpoint of the period and that all individuals are dead by the time of the final sampling occasion (assumptions A1 and A2 above).

Except in the simulation with $R = 200$, $K = 5$, and $P = 0.5$ (Table 3), the estimated variance using the delta method was a good indicator of the true variance as reflected in the sample variance. This was true for both the parametric and nonparametric estimators.

© 1998 NRC Canada

Table 5. Nonparametric estimates of the survival probabilities and detection probabilities for spawning sockeye salmon in Iliamna Lake, Alaska (Quinn and Foote 1994) (equivalent to Cormack (1964) and Burnham et al. (1987) estimates).

Day (sampling occasion)	$\hat{S}_i$			$\hat{P}_i$		
	Males	Females	Overall	Males	Females	Overall
1	1.000	1.000	1.000			
2	1.000	1.000	1.000	0.663	0.866	0.754
3	0.996	1.000	0.995	0.555	0.598	0.574
4	0.915	0.991	0.952	0.848	0.976	0.908
5	0.979	0.960	0.966	0.787	0.910	0.844
6	0.927	0.962	0.943	0.793	1.000	0.892
7	0.810	0.869	0.831	0.891	1.000	0.946
8	0.586	0.828	0.713	0.850	0.982	0.926
9	0.525	0.685	0.617	1.000	1.000	1.000
10	0.381	0.595	0.517	1.000	1.000	1.000
11	—	0.273	0.233	1.000	1.000	1.000
12				—	1.000	1.000

The nonparametric estimator had a significant negative bias in simulations with a high level of right censoring (Table 2). The level of right censoring had little detrimental effect on the parametric estimator.

The parametric estimator was unstable and often failed completely to estimate the parameters with low sample size, small number of sampling occasions, and a low detection probability (Table 3). However, when the factors that are under direct human control (sample size and number of sampling occasion) are increased, the parametric estimator performs adequately.

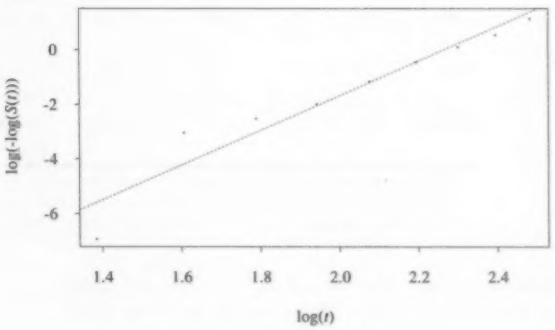
The parametric estimator was shown to be reasonably robust to deviations from the assumed Weibull distribution (Table 1). For simulations with lifetimes generated from a gamma distribution, the parametric estimator was actually significantly less biased than the nonparametric estimator. For lifetimes generated from the stream 16131 empirical distribution, which would appear to adhere closer to a Weibull distribution than the gamma distribution (compare Figs. 1*b* and 2), the nonparametric estimator was slightly more precise and less biased.

Analysis of Iliamna Lake sockeye salmon example

To estimate the stream residence time of Iliamna Lake sockeye salmon (Quinn and Foote 1994) using the nonparametric estimator, the number detected per occasion and the number detected for the last time per occasion were tabulated (Table 4), and the nonparametric estimates of the survival probabilities (S_i), along with the estimates of the detection probabilities (P_i), were calculated (Table 5). From these estimates, the nonparametric estimate of stream residence time was calculated from eq. 1 as $\hat{T} = 7.968$, with standard error $\hat{\mathrm{SE}}(\hat{T}|T) = 0.1429$.

Before calculating the parametric estimate of stream residence time, the log–log plot of the empirical survival function as a function of log(t) was plotted (Fig. 3) to determine if the Weibull distribution was an appropriate model for these data. Again, there is evidence that the Weibull distribution is a good model for the lifetimes of spawning salmon.

Fig. 3. Log–log plot of the empirical survival function for Iliamna Lake sockeye salmon, along with the optimal least squares line.



Optimization of the likelihood function for the parametric estimator (eq. 4) yields the estimates $\hat{\alpha} = 0.114$ and $\hat{\beta} = 4.678$. The resulting parametric estimate of stream residence time, using eq. 5, is $\hat{T}_P = 8.023$ with standard error $\hat{\mathrm{SE}}(\hat{T}_P|T) = 0.1471$.

The stream residence time of the 82 females and 101 males in the population can be estimated separately and compared. Unfortunately, the variance calculation for the parametric estimator for the males resulted in a negative value, presumably because of the small sample size. Therefore, the nonparametric estimator was used. The nonparametric estimate of stream residence time for the females is $\hat{T}_F = 8.602$, with standard error $\hat{\mathrm{SE}}(\hat{T}_F|T) = 0.2041$. Similarly for the males, $\hat{T}_M = 7.475$, with standard error $\hat{\mathrm{SE}}(\hat{T}_M|T) = 0.1819$. The null hypothesis that there is no difference is stream residence time can be tested with a two-sample Z test as follows:

$$Z = \frac{\hat{T}_F - \hat{T}_M}{[(\hat{\mathrm{SE}}(\hat{T}_F|T))^2 + (\hat{\mathrm{SE}}(\hat{T}_M|T))^2]^{1/2}} = 4.122.$$

The p value based on a Normal distribution is 0.00002, strongly supporting the alternative hypothesis that the stream

© 1998 NRC Canada

residence time for females is significantly different from that for males.

Recommendations and conclusion

In designing a study for estimating stream residence time, care should be given to ensure an adequate sample size and an adequate number of sampling occasions. The Monte Carlo simulations in this paper indicate that with an adequate sample size and number of sampling occasions, both estimators provided precise estimates of stream residence time and provided adequate estimates of the variance of the estimate.

Once the conditional survival probabilities (S_i) have been estimated, a log–log plot of the empirical survival function can be plotted to examine how well it follows a Weibull distribution. If it is reasonably close to a Weibull distribution, the parametric estimator should be used. Otherwise, the nonparametric estimator should be used except as noted below.

If a significant number of individuals are believed to be alive at the end of the study, the parametric estimator should be used, even if the empirical survival function deviates significantly from a Weibull distribution. Note, however, that since iterative, numerical procedures must be used to estimate the parameters for the parametric estimator, there is a chance that it will fail to estimate the parameters, and the nonparametric estimator must be used.

Both estimators are capable of providing precise, statistically valid estimates of stream residence time. In addition, both estimators provide an estimate of the variance, allowing the precision of the estimate to be assessed and allowing for statistical inference and hypothesis testing. Both estimators are also applicable to estimating the life expectancy of other fish and wildlife populations using release–recapture techniques.

Acknowledgments

We thank Thomas P. Quinn and Chris J. Foote for providing the data from the 1994 Iliamna Lake sockeye salmon study.

References

Ames, J. 1984. Puget Sound chum salmon escapement estimates using spawner curve methodology. *In* Proceedings of the Workshop on Stream Indexing for Salmon Escapement Estimation. *Edited by* P.E.K. Symons and M. Waldichuk. Can. Tech. Rep. Fish. Aquat. Sci. No. 1326.

Beidler, W.M., and Nickelson, T.E. 1980. An evaluation of the Oregon Department of Fish and Wildlife Standard Spawning Fish Survey System for coho salmon. Oreg. Dep. Fish Wildl. Inf. Rep. 80-9.

Burnham, K.P., Anderson, D.R., White, G., Brownie, C., and Pollock., K.H. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society, Bethesda, Md.

Cormack, R.M. 1964. Estimates of survival from sighting of marked animals. Biometrika, **51**: 429–438.

Crosbie, S.F., and Manly, B.F.J. 1985. Parsimonious modelling of capture–mark–recapture studies. Biometrics, **41**: 385–398.

English, K., Bocking, R.C., and Irvine, J.R. 1992. A robust procedure for estimating salmon escapement based on the area-under-the-curve method. Can. J. Fish. Aquat. Sci. **49**: 1982–1989.

Lady, J.M. 1996. Release–recapture models for estimating the stream residence time of spawning salmon. M.S. thesis, University of Washington, Seattle, Wash.

Lawless, J.F. 1982. Statistical models and methods for life time data. John Wiley & Sons, New York.

Liao, S. 1994. Statistical models for estimating salmon escapement and stream residence time based on stream survey data. Ph.D. thesis, University of Washington, Seattle, Wash.

Maki, A.W., Brannon, E.J., Gilbertson, L.G., Moulton, L.L., and Skalski, J.R. 1995. An assessment of oil spill effects on pink salmon populations following the *Exxon Valdez* oil spill — Part 2: Adults and escapement. *In Exxon Valdez* oil spill: fate and effects in Alaskan waters. *Edited by* P.G. Wells, J.N. Butler, and J.S. Hughes. American Society for Testing and Materials, Philadelphia, Pa. pp. 585–625.

Perrin, C.J., and Irvine, J.R. 1990. A review of survey life estimates as they apply to the area-under-the-curve method for estimating the spawning escapement of Pacific salmon. Can. Tech. Rep. Fish. Aquat. Sci. No. 1733.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., and Flannery, B.P. 1992. Numerical recipes in C: the art of scientific computing. 2nd. ed. Cambridge University Press, Cambridge, U.K.

Quinn, T.P., and Foote, C.J. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. Anim. Behav. **48**: 751–761.

© 1998 NRC Canada

Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake

David M. Post, James F. Kitchell, and James R. Hodgson

Abstract: Using 12 years of data, we evaluated the mechanisms controlling largemouth bass, *Micropterus salmoides*, recruitment in a lake near the northern extent of the largemouth bass range. We found that complex interactions among adult demographics, size-selective predation, and overwinter mortality regulate the number of largemouth bass surviving the first year of life. The largest recruitment events required at least a moderate number of adults, but a large number of adults was not sufficient to produce a large cohort of largemouth bass. Predation was controlled by the number of both adult and juvenile bass and was not strongly correlated with reproductive output. Overwinter mortality was size dependent, strongly affecting bass entering the winter at <50–60 mm in length, and likely the result of starvation. Predation and overwinter mortality interacted with spawning date and growth rate to produce variable but predictable patterns of first year survival. At high adult and juvenile densities, predation regulates first year survival. At low adult and juvenile densities, first year survival was regulated by adult demographics and interactions among spawning date, growth rates, and overwinter mortality. Although we can forecast coarse patterns of cohort survival, the survival of individual fish was more difficult to predict because length and age were not highly correlated.

Résumé : À partir de données s'étalant sur 12 ans, nous avons évalué les mécanismes régissant le recrutement de l'achigan à grande bouche, *Micropterus salmoides*, dans un lac situé près de la partie septentrionale de l'aire de répartition de ce poisson. Nous avons observé que des interactions complexes entre les paramètres démographiques des adultes, la prédation selon la taille et la mortalité hivernale déterminent le nombre d'achigans qui survivent plus d'un an. Les recrutements les plus importants étaient obtenus quand il y avait au moins un nombre modéré d'adultes, mais la présence d'un grand nombre d'adultes n'était pas suffisant pour produire une cohorte importante d'achigans. La prédation était régie par le nombre d'adultes et de juvéniles et n'était pas fortement corrélée avec la production génésique. La mortalité hivernale était fonction de la taille et touchait fortement les achigans dont la longueur au début de l'hiver était de moins de 50 à 60 mm; elle était probablement attribuable à l'inanition. La prédation et la mortalité hivernale étaient reliées à la date de fraye et au taux de croissance, d'où des profils de survie durant la première année variables mais prévisibles. Quand les densités des adultes et des juvéniles étaient élevées, la prédation déterminait la survie durant la première année. Quand ces densités étaient basses, la survie durant la première année était déterminée par les caractéristiques démographiques des adultes et les interactions entre la date de fraye, les taux de croissance et la mortalité hivernale. Bien que nous ayons pu prévoir les caractéristiques générales de la survie des cohortes, la survie des individus était plus difficile à prévoir parce que la longueur et l'âge n'étaient pas fortement corrélés.

[Traduit par la Rédaction]

Introduction

Fish recruitment is problematic for fish ecologists and fisheries managers because it is inherently variable and difficult to quantify (e.g., Fogarty et al. 1991). Despite these difficulties, the emerging paradigm is that recruitment is regulated by the interaction of density-dependent and density-independent mortality involving size-dependent processes at early life history stages (e.g., Sissenwine 1984; Houde 1987). For this reason, mechanistic studies focusing on survival of fish in their first days, weeks, and months of life are critical to understanding recruitment variability (Crowder et al. 1992). A holistic approach has been called for (Sissenwine 1984), but few studies have assessed the constraints on recruitment for more than a short period of life and most have evaluated only one or a few of the potential mechanisms (however, see Elliott 1984).

This study focuses on largemouth bass, *Micropterus salmoides*, a geographically widespread fish species that supports recreational fisheries throughout its range. Recruitment of largemouth bass is highly variable (Summerfelt 1975).

Received October 9, 1996. Accepted September 11, 1998.
J13693

D.M. Post[1] **and J.F. Kitchell.** Center for Limnology, University of Wisconsin – Madison, Madison, WI 53706, U.S.A.
J.R. Hodgson. Department of Biology, St. Norbert College, De Pere, WI 54115, U.S.A.

[1]Author to whom all correspondence should be addressed. Present address: Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, NY 14853, U.S.A.
e-mail: dmp18@cornell.edu

© 1998 NRC Canada

Largemouth bass are well studied and provide an ideal subject for studying how the interaction of density-dependent and density-independent mechanisms influence fish recruitment. Most individual mechanisms have been documented, but no study has yet integrated observations on multiple mechanisms in a single system.

Multiple mechanisms are likely to interact hierarchically to regulate recruitment. Adult demography strongly influences the number of eggs spawned and is the ultimate constraint on recruitment potential. The number of largemouth bass that survive the first year of life, however, seldom correlates strongly with the number of young spawned. Predation during summer months and overwinter mortality are considered common sources of mortality and likely constrain recruitment through the first year of life. These sources of mortality are size selective and therefore interact with spawning date and growth rates, two factors that govern size at age (e.g., Miller and Storck 1984). In general, rapid growth and large size reduce the risk of predation (e.g., Miller et al. 1988; Luecke et al. 1990) and lower the probability of overwinter mortality resulting from starvation (e.g., Oliver et al. 1979; Miranda and Hubbard 1994*a*). However, these constraints do not operate independently. Modeling efforts suggest that predation may interact strongly with growth rates through a density-dependent growth response and therefore influence overwinter survival (DeAngelis et al. 1991). Model results suggest that increased predation could increase growth, which would increase the probability of overwinter survival. While strongly suggestive, these results remain untested.

Here we evaluate the mechanisms influencing recruitment of largemouth bass in a lake near the northern extent of the largemouth bass range. We show that the number of bass surviving the first year of life results from complex interactions among adult demography, spawning date, young-of-the-year growth rates, predation, and overwinter mortality. We estimate the major sources of mortality and test the theory that size-selective mortality differentially affects the survival of fish of different ages. Our results are placed in the context of both individual and cohort survival. Finally, we discuss the effects of largemouth bass recruitment on long-term population dynamics, fish community dynamics, and food web structure.

Methods

Study site

Paul Lake is a small (1.7 ha, maximum depth 15.0 m), oligotrophic lake located at the University of Notre Dame Environmental Research Center, Gogebic County, Michigan, U.S.A. Paul Lake is located near the northern extent of the largemouth bass range and largemouth bass dominate the fish community (>95% of the fish biomass). This population of largemouth bass has been unmanipulated and unexploited since it was established in 1976 (Leavitt et al. 1989). Paul Lake and its history are fully described in Leavitt et al. (1989) and Carpenter and Kitchell (1993).

Fish population estimates

All bass ≥150 mm in total length (TL) were marked with individually numbered Floy tags. Fish ≥300 mm TL (4–5 years of age) were considered reproductively mature adults (Scott and Crossman 1973). Individuals <300 mm TL and at least 1 year old were considered juveniles. All bass in the first year of life were considered young-of-the-year (YOY). Population estimates of juvenile and adult bass were conducted in mid-May and mid-August of each year using Petersen or Schnabel mark–recapture methods (Krebs 1989). Schnabel mark–recapture estimates were used when multiple recapture events were possible. To minimize recapture bias, marks and recaptures were conducted using a combination of angling and electroshocking. The mark for fish ≥150 mm was their individually numbered Floy tag and the mark for fish <150 mm was a clipped caudal fin. Annual population densities for juveniles and adults were calculated as the average of May and August population estimates.

Mark–recapture population estimates for YOY largemouth bass were made in mid-August. Because angling was not possible for YOY bass, all marks and recaptures were made by electroshocking. The mark for YOY bass was a caudal fin clip. Standard error estimates for YOY populations were estimated according to Krebs (1989). When mark–recapture population estimates were not available, the abundance of YOY largemouth bass was estimated from the relationship between catch per unit effort and mark–recapture estimates from other years (population estimate = 8.3 · number caught − 156.7; $N = 7$; $R^2 = 0.94$). We used the standard error estimate for predicted values around the fitted regression for the standard error of these population estimates (Draper and Smith 1981). The entire shoreline was sampled when electroshocking for population estimates. Effort was the number of times that the entire lake was shocked.

The number of YOY largemouth bass at swim-up was estimated using two techniques: direct nest counts and estimates reconstructed indirectly from predation estimates (Forney 1977). Nest count estimates were derived from the number of successful nests and an estimate of the average number of fry per nest (3000, range 2000–7000; Scott and Crossman 1973). Nest surveys were conducted by underwater observation (snorkeling). Nest surveys were conducted in 1993–1995 from late May until all eggs had hatched and nest schools of fry were dispersed. The entire lake was surveyed once every 2–3 days. All nests were counted and the stage of YOY largemouth bass development was recorded. The hatching dates of nests with eggs that hatched between observations were corrected by 1–2 days based on developmental stage of fry. We defined a successful nest as a nest that produced swim-up fry and a nest school.

We sampled YOY largemouth bass throughout the summers of 1993–1995 using dip nets and electroshocking. Samples were collected by dip netting while nest schools persisted. After the schools dispersed, YOY largemouth bass were sampled by electroshocking. YOY largemouth bass between 15 and 25 mm TL were generally not vulnerable to the combination of dip netting and electroshocking. Fish longer than 25 mm were vulnerable to electroshocking and were sampled accordingly. All YOY largemouth bass were measured to the nearest 1 mm.

Forney (1977) demonstrated that, when accurate predation estimates can be made, the number of YOY fish hatched can be closely estimated by the cumulative number of YOY fish eaten plus the number of YOY alive at that time. In Paul Lake, adult and juvenile bass are the only important predators of YOY bass. Our predation estimates derive from whole-lake, mark–recapture population estimates for adult and juvenile bass, regular sampling to collect diet information, and a well-corroborated bioenergetics model (Rice and Cochran 1998; Whitledge and Hayward 1997). Our cumulative predation estimates plus August mark–recapture estimates are a good estimate of the number of YOY bass hatched in each year. There is a strong correlation ($r = 0.98$) between estimates of the number of YOY hatched (as derived from nest counts) and from predation estimates in 1993–1995. There is uncertainty around this relationship because we have assumed an average number of fry per nest and because there is error associated with our

© 1998 NRC Canada

adult and juvenile population estimates. However, the range of possible nest-count-based estimates and cumulative-predation estimates overlap almost completely (see Table 2).

Diet information

In 1984–1995, we collected diet data from adult and juvenile largemouth bass to estimate predation on YOY bass. Diet data were collected by angling and electroshocking. Samples were taken each year between mid-May and late August at intervals of 2–3 weeks. Samples were collected between 0800 and 1130 h, and 1600 and 2000 h. The mean sample size was 26 (SE = 1.2). Diets were generally similar between morning and evening samples. Statistical analysis of sample size and intra- and inter-sample diet variance are presented elsewhere (Hodgson and Cochran 1988; Hodgson et al. 1989). Stomach contents were flushed from the stomach with water, collected in a 0.28 mm mesh concentrator, and preserved in 95% ethyl alcohol. Diet collection techniques are fully described in Carpenter and Kitchell (1993). All diet items were identified to the lowest relevant taxonomic group and enumerated. Diets were analyzed as percent composition by wet mass using standardized weights for each prey item (Carpenter and Kitchell 1993).

Predation estimates

Predation by adults and juveniles on YOY largemouth bass was estimated using the bioenergetics approach of Kitchell et al. (1977), with largemouth bass parameters from Rice et al. (1983) and Trebitz (1991). Modeling was conducted with the generalized fish bioenergetics software developed by Hewett and Johnson (1992). Water temperatures for this model were from weekly temperature profiles taken each year from May through September. We assumed that largemouth bass experienced water temperatures comparable with those recorded at a depth of 1 m. Adult and juvenile energy densities were assumed to be 1000 cal·g wet mass^{-1} (Hewett and Johnson 1992).

We quantified the relationship between adult and juvenile cannibalism and YOY largemouth bass abundance by comparing adult and juvenile diets with YOY abundance in August of each year. We used the asymptotic model

$$(1) \qquad Y = a \cdot [1 - \exp^{(-b \cdot X)/a}]$$

where Y was the percent (by mass) of YOY largemouth bass in the diet of adults and juveniles, X was the abundance of YOY largemouth bass in Paul Lake, and a and b were free parameters describing the asymptote and slope of the curve, respectively. The asymptote, a, represents the maximum percent of YOY largemouth bass in the diets of adult and juvenile bass. Because this relationship contained errors in the predictors, we weighted each data point by the inverse of its variance and fit the model using negative log likelihood (Clutton-Brock 1967; Reilly and Patino-Leal 1981). Parameter standard errors were calculated by bootstrapping residuals (Efron and Tibshirani 1993).

To quantify the impact of cannibalism on recruitment, we compared our direct and indirect estimates of the number of YOY hatched to predation estimates and an estimate of the maximum potential predation. Predation estimates derive from bioenergetic calculations using the observed temperatures, growth rates, and diet composition of adult and juvenile bass in each year. They represent our best estimate of the total number of YOY bass eaten from hatching through late August. Our estimates of maximum potential predation represent the maximum number of YOY bass that could have been eaten in each summer. We calculated the maximum potential predation in each year using observed temperatures and growth rates but assumed that adult and juvenile diets contained the maximum percent of YOY largemouth bass possible (estimated by a from eq. 1) for the period from the first incidence of YOY largemouth bass in adult and juvenile diets to late August. By holding everything except diet composition constant, maximum potential predation represents the number of YOY largemouth bass that could have been eaten in a summer had there been at least that many YOY hatched. Dividing the number of YOY eaten by the maximum potential predation provides a useful index of the intensity of predation. When this index is low, adult and juvenile bass could have eaten many more YOY than they did. When this index is high (approaching 100%), adults and juveniles were eating as many YOY as they could. Because of uncertainty of our population estimates and our estimate of a, we would not expect our estimates of predation and maximum potential predation to be equal.

We sampled in 1993 and 1994 to assess prey size selectivity by adult and juvenile bass. A length frequency distribution of YOY largemouth bass was collected from Paul Lake within a day of collecting adults and juveniles for diet analysis. We measured the TL or standard length (SL; length from snout to the end of the vertebral column) of all measurable fish found in adult and juvenile stomachs. Standard lengths were converted to total length using the relationship

$$TL = 1.19 \cdot SL - 0.37 \qquad (n = 34,\ R^2 = 0.99,\ P < 0.01)$$

The total length of fish from diet samples preserved in 95% ethyl alcohol were corrected for shrinkage using the relationship

$$TL_F = 1.07 \cdot TL_P - 1.25 \qquad (n = 26,\ R^2 = 0.97,\ P < 0.01)$$

where TL_F was the fresh (unpreserved) total length and TL_P was the preserved total length. We did not correct for variable storage time because all preserved fish were measured after they had been preserved for >1 year.

We used the Kolmogorov–Smirnov test (Sokal and Rohlf 1981) to test the null hypothesis that the length frequency distributions from diet samples were the same as length frequency distributions of YOY largemouth bass in the lake. A non-significant result indicates that adults and juveniles were selecting YOY largemouth bass at random, and a significant result indicates that predation was size selective. The in-lake length frequencies for 23 June, 30 June, and 7 July in 1994 are likely biased because of sampling limitations. The sample on 23 June does not include large, early-spawned fish from dispersed nest schools, and samples on 30 June and 7 July may underrepresent fish <25 mm because they are difficult to accurately sample with electroshocking techniques. These biases, however, do not change our interpretation of the results.

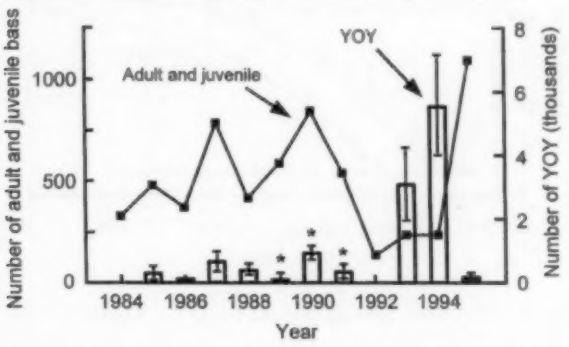
Growth rate estimates

Otolith microstructures were analyzed to evaluate age-specific growth rates and to estimate age-dependent summer survival. The daily rings of largemouth bass otoliths (sagittae) provide a reliable estimate of age for fish in their first summer of life (e.g., Miller and Storck 1982). We collected YOY largemouth bass for otolith analysis in late August of 1993 and 1994. Over 100 fish were haphazardly collected in each year. Otoliths were prepared according to the methods of Miller and Storck (1982) and Isley and Nobel (1987). The number of daily rings in each otolith was counted a minimum of three times. If the three counts were within one day, the mode was taken as the age. If the three counts were not within one day, the otolith was aged an additional 2–4 times and the mode was used as the age. For >90% of all otoliths, an age mode was evident after 3 to 5 counts. Based on our observations and previous studies (Miller and Storck 1982; Isely and Noble 1987), we believe that our otolith-based age estimates are accurate to ±3 days.

The pattern of age-dependent mortality over the summer was estimated using the chi-squared test for goodness of fit (Sokal and

© 1998 NRC Canada

Fig. 1. Population dynamics of Paul Lake largemouth bass for 1984–1995. The population estimates for adults and juveniles are the summer average. The YOY largemouth bass estimates are from August only (±1 SE). Estimates in some years (*) derive from the relationship between catch per unit effort and population estimates for young-of-the-year in the other years.



Rohlf 1981) to compare the age distribution of fish sampled in late August (from otolith analysis) to the hatching date distribution of successful nests. We assigned surviving fish and successful nests to early- and late-hatched categories. The division for early and late hatched was based on the median hatching date for each year. Only two categories were used to increase sample size and to minimize the effects of otolith aging errors.

Overwinter mortality

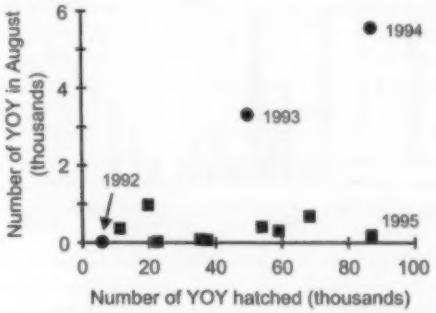
We assessed the pattern of overwinter mortality by sampling the 1993 and 1994 cohorts in early October after water temperatures were <10°C and in May just after temperatures reached 10–12°C. Largemouth bass growth is minimal at water temperatures <10°C (Johnson and Charlton 1960; Coutant 1975). We collected >150 fish on each sampling date when possible. All fish were measured to the nearest 1 mm TL and weighed to the nearest 0.01 g on an analytical balance. We used the Kolmogorov–Smirnov test to test the null hypothesis that spring and fall length frequency distribution were the same. We then used quantile–quantile plots to differentiate size-selective mortality from growth and to determine the pattern of size-selective mortality when detected (Post and Evans 1989). Data points used in quantile–quantile plots were taken at 1, 5, 10, 25, 50, 75, 90, 95, and 99% of the length distributions for each cohort in the fall and spring. Regressions through quantile–quantile data points were fit using least squares and were tested for significant deviations from a slope of one and an intercept of zero (Draper and Smith 1981).

To evaluate the prospect that overwinter mortality was caused by starvation, we tested for declines in condition factor from fall to spring for the 1993 and 1994 cohorts. We also compared spring length distributions with those predicted by the physiologically based overwinter mortality model of Shuter et al. (1980). For this model, we assumed winter duration of 150 days in 1993 and 145 days in 1994 (number of days with water temperature <5°C). Winter duration was estimated from water temperature data taken by the North Temperate Lakes Long Term Ecological Research Project in lakes located about 30 miles south of Paul Lake.

We used data from both the 1993 and 1994 cohorts to estimate the general relationship between overwinter survival and total length in Paul Lake. We used the sigmoidal relationship:

$$\text{relative survival} = \frac{\text{length}^a}{\text{length}^a + b^a}$$

Fig. 2. Relationship between the number of YOY bass in August and the number of YOY bass hatched for the years 1984–1996. Years with low adult and juvenile abundance are shown with circles and years with high adult and juvenile abundance are shown with squares.



where relative survival was the percentage of fish surviving the winter and length was total length (mm) entering the winter. We grouped fish by 5 mm length categories and then calculated relative survival (number of fish in fall divided by the number of fish in spring) from fall to spring for each length group. Because the sample size of each length category varied, each data point was weighted by its sample size. The model was fit using the nonlin module in SAS (SAS Institute 1985).

Results

Over the 12-year period, the abundance of adult and juvenile bass fluctuated between 131 and 1095 individuals (Fig. 1), with biomass roughly paralleling adult densities. Adult and juvenile abundance was high in 1984–1991, low in 1992–1994, and high again in 1995 (Fig. 1). Adult and juvenile bass were three times more numerous in high abundance years than low abundance years [604 ± 255 vs. 200 ± 60 individuals, respectively ($\bar{x}$ ± SD)]. The number of YOY largemouth bass surviving to late August of each year ranged from a few hundred individuals in 1984–1992 and in 1995 to several thousand in 1993 and 1994 (Fig. 1).

There was a strong correlation between the number of reproductively mature adult bass in spring of each year and both the number of nests (n = 3, r = 0.99, P = 0.09) and the number of YOY hatched (n = 12, r = 0.70, P = 0.01; estimated from predation estimates) but not with the number of YOY bass surviving to August (n = 12, r = 0.07, P = 0.82). There was no correlation between the number of YOY largemouth bass hatched and the number of YOY surviving to August (n = 12, r = 0.46, P = 0.11; Fig. 2). The number of YOY bass hatched was, therefore, strongly related to the number of reproductively mature adult bass, but the number of YOY bass hatched was not a strong predictor of survival through the summer.

Hatching dates and growth rates

In 1993–1995, successful hatching occurred over a range of 41 days beginning in mid- May and ending in early July (Fig. 3). Within a single year, the duration of successful hatching dates was 17 to 21 days. In 1994 and 1995, hatching was early, while in 1993, hatching occurred relatively late (Fig. 3). The temporal pattern of hatching across and

© 1998 NRC Canada

Fig. 3. Hatching date distributions for the 1993–1995 YOY bass cohorts (cross-hatched bars, 1993; open bars, 1994; solid bars, 1995). Each point represents the hatching date of one successfully hatched nest.

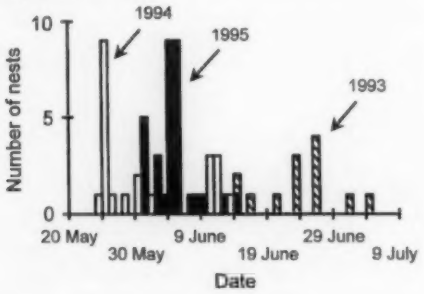
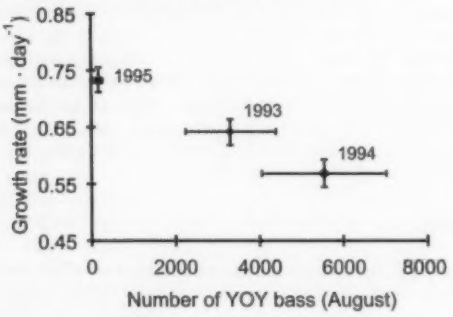


Fig. 4. Growth rates (±95% CI) and late August densities (±1 SE) of the 1993–1995 YOY bass cohorts.



within years was generally consistent with water temperature patterns. For example, the spring of 1993 was cold and hatching was postponed until late June and early July. In contrast, Paul Lake warmed rapidly in 1994 and 1995 and hatching dates were earlier. A cold snap during late May and early June of 1994 caused a bimodal hatching distribution.

Average summer growth rates (from hatching to late August) of YOY largemouth bass were inversely related to cohort density (Fig. 4). Growth rates were similar for fish <25 mm, but after reaching 25 mm growth trajectories diverged (Fig. 5). Across years, individual length increased with age (Fig. 6). Otolith analysis demonstrated that each additional day of growth (as a result of an earlier hatching date) added an average of 0.53 mm in length. However, age explained only 38% and 17% of the variability in length in 1993 and 1994, respectively, and the variability of length increased with age (Fig. 6). Although young fish tended to be of small to average size, older fish spanned the entire range of lengths from the smallest to largest (Fig. 6). Thus, the largest fish were all older individuals and small- to medium-sized fish ranged in age from the oldest to the youngest.

Patterns of summer mortality

We used otoliths from fish sampled in late August to infer patterns of summer mortality with respect to fish age. There were differences between the observed hatching date distribution and the back-calculated hatching date distribution in 1993 (chi-square test for goodness of fit, $\chi^2 = 56.6$, $P < 0.05$) and 1994 ($\chi^2 = 6.4$, $P < 0.05$). In both years, late-spawned fish were underrepresented in late August samples (Table 1), indicating differentially high mortality among later-spawned individuals.

Fig. 5. Growth trajectories of the 1993–1995 YOY bass cohorts (squares, 1993 cohort; diamonds, 1994 cohort; open circles, 1995 cohort). Error bars are ±1 SD.

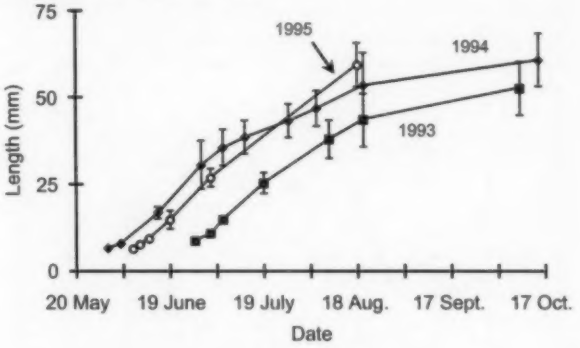


Fig. 6. Relationship between age and length for members of the 1993 and 1994 YOY bass cohorts (on 20 August). Age estimates are from otolith analysis. The dotted line is the approximate size required (in August) to survive the winter (~47 mm, assuming 8 mm of growth from late August to winter). See text for a further discussion.

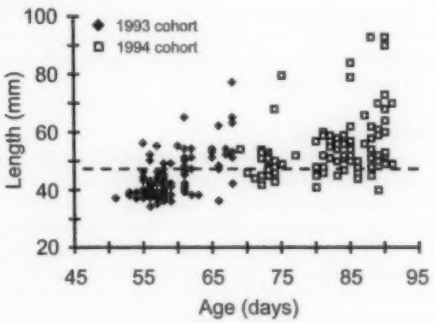


Table 1. Temporal distribution of hatching dates of successful nests and fish surviving the summer for 1993 and 1994.

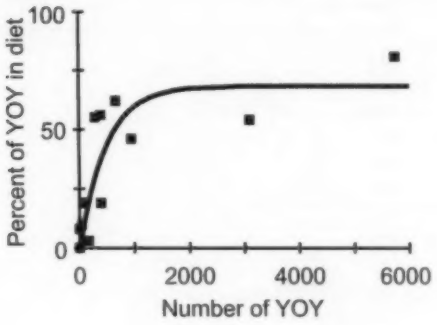
Year and hatching period	Nests, %	Fish, %
1993		
Early hatched (before 24 June, ≥57 days old)	46	74
Late hatched (after 24 June, <57 days old)	54	26
1994		
Early hatched (before 3 June, ≥80 days old)	68	75
Late hatched (after 3 June, <80 days old)	32	25

Cannibalism

YOY largemouth bass were an important component of the adult and juvenile diets when YOY were abundant in the lake (i.e., greater than a few hundred individuals, Fig. 7). At

© 1998 NRC Canada

Fig. 7. Relationship between the percentage of YOY in adult and juvenile bass diets (by mass) and YOY bass densities in August of 1984–1996.



densities above ~1000 YOY, cannibalism represented about 68% of adult and juvenile diets. The relationship was described by the function

$$Y = 68.2 \cdot [1 - \exp^{(-0.139 \cdot X)/68.2}] \qquad (R^2 = 0.65)$$

where Y was the proportion of YOY in adult and juvenile diets, and X was the August density of YOY largemouth bass. The parameter estimates and standard errors were: a = 68.2 (11.2) and b = 0.139 (0.066).

Predation can account for all of the observed mortality in 1993–1995, years in which we have independent estimates of the number of YOY hatched and the number of YOY eaten, although there is some uncertainty associated with our estimates (Table 2). This confirms that adult and juvenile bass were the only important predators of YOY and that the number of YOY eaten plus the number of YOY alive in August is a good estimate of the number of YOY hatched.

Juvenile bass were the most important predators in Paul Lake. Around 90% of the cannibalism in each year was caused by juvenile bass (mean 92%, range 82–99%). In some years, for example, 1995, most of the cannibalism by juvenile bass was caused by bass in their second summer of life (age 1+).

In years of high adult and juvenile abundance (1984–1991 and 1995), predation on YOY largemouth bass was intense, and adult and juvenile bass could have eaten many more YOY than were hatched (Table 2). Predation rapidly eliminated most of the YOY cohort in these years. In 1995, for example, predation eliminated 98% of the YOY cohort in less than 4 weeks. The largest recruitment events occurred in years of low adult and juvenile abundance (Fig. 1). In 1993 and 1994, the number of YOY eaten and the maximum potential predation were similar, indicating that adult and juvenile bass diets were saturated with YOY (Table 2). It would have been difficult for adult and juvenile bass to eat more YOY bass than they did. The YOY that survived the summers of 1993 and 1994 were those that adult and juvenile bass were unable to eat by late August. The exception to this pattern was the summer of 1992. Although adult and juvenile abundance was low in 1992, the number of reproductively mature adults was extremely low and the number of YOY hatched was the lowest recorded (Fig. 2). There was no measurable survival of YOY through the summer of 1992 (Fig. 1).

When the number of predators is high, the number of YOY surviving the summer is low. The predation potential in these years is much higher that the potential reproductive output. When the number of predators is low, the number of YOY surviving the summer can be high but is clearly mediated by the number of YOY hatched (Fig. 2). The number of YOY hatched was a good predictor of August YOY abundance in years with low adult and juvenile abundance (R^2 = 0.998, n = 3) but not in years with high adult and juvenile abundance (R^2 = 0.002, n = 9). Thus, large year-classes (estimated in August of their first year) occurred only when predation was low and reproductive output was relatively high (Fig. 2).

There is no absolute size refuge from cannibalism for YOY largemouth bass in Paul Lake. Based on an average adult and juvenile length of 235 ± 52.1 mm ($\bar{x}$ ± SD, 1984–1995) and a predator–prey maximum size ratio for cannibalism of 2:1 (Lawrence 1958), bass must reach at least 118 mm in length before obtaining a size refuge from the average cannibalistic bass. In their first year of life, largemouth bass in Paul Lake reach 75 ± 10.7 mm in length (1984–1995).

Cannibalism by adult and juvenile bass was size selective (Fig. 8). Initially, adult and juvenile largemouth bass selected the largest individuals in the cohort. However, dispersed fish between 15–30 mm TL were not vulnerable to dip-net sampling and are not represented in the 23 June 1994 length frequency distribution. After all nest schools had dispersed, predators selected fish that were smaller than the average size, although larger fish were taken on occasion (Fig. 8).

Overwinter mortality

We detected strong size-selective overwinter mortality in the 1993 cohort (Fig. 9*a*). The 1993 cohort entered the winter of 1993–1994 with median and modal lengths of 50 and 48 mm, respectively. However, few individuals <55 mm survived the winter. The fall and spring distributions were significantly different (Kolmogorov–Smirnov test, $P < 0.05$, D = 0.727, $D_{\alpha=0.05}$ = 0.263), and quantile–quantile plots indicated size-selective mortality on smaller individuals over the winter (H_0: slope = 1, n = 9, t = –2.8, $P < 0.05$). The result of this size-selective overwinter mortality was the virtual elimination of the 1993 cohort. Only 74 (31–215, 95% CI) of 3303 (1789–6167) bass from the 1993 cohort survived the period from late August to May. This corresponds to an overwinter survival rate of only 2.2%.

Members of the 1994 cohort entered the winter at a much larger size and did not suffer significant size-selective overwinter mortality (Fig. 9*b*). The fall and spring length distributions were similar (Kolmogorov–Smirnov test, P = 0.19, D = 0.116, $D_{\alpha=0.05}$ = 0.145), and quantile–quantile plots indicated no size-selective mortality and little growth over the winter (H_0: slope = 1, n = 9, t = –1.9, P = 0.1; H_0: intercept = 0, n = 9, t = 2.5, P = 0.04). As a result, the 1994 cohort had much higher survival over winter than the 1993 cohort. An estimated 1465 (942–3296) of 5551 (3587–9757) bass from the 1994 cohort survived the period from late August to May (26.4% survival).

© 1998 NRC Canada

Table 2. Estimates of the number of YOY bass hatched and eaten and the maximum potential number of YOY bass eaten.

Year	Young-of-the-year bass (in thousands)				Number eaten as percent of maximum potential
	Number hatched (range)[a]	Number hatched (range)[b]	Number eaten (range)[c]	Maximum potential number eaten (range)[d]	
1984		22	22	243	9
1985		59	58	281	21
1986		37	37	173	21
1987		68	67	321	21
1988		53	53	270	20
1989		35	35	198	18
1990		19	18	127	14
1991		11	10	178	6
1992		5	5	51	10
1993	45	57	54	64	84
	(30–105)	(35–104)	(33–98)	(40–117)	
1994	66	68	62	78	80
	(40–154)	(42–152)	(38–142)	(52–173)	
1995	99	94	94	333	28
	(66–231)	(52–191)	(52–190)	(203–700)	

Note: For 1993–1995, we present a range of possible estimates. The number of YOY bass eaten as a percent of the maximum potential number of YOY bass eaten is an index of how saturated adult and juvenile bass diets were by YOY bass. A low percentage indicates that adult and juvenile bass could have easily eaten all of the YOY hatched in that year and probably did so rapidly. A high percentage indicates that adult and juvenile bass were feeding on YOY bass near their maximum possible rate.

[a]Estimated from nest counts and assuming 3000 fry per nest (range 2000–7000).

[b]The number of YOY eaten by late August plus the number of YOY alive at that time is an index of the number of largemouth bass hatched in that year. Note the strong correlation ($r = 0.99$) and nearly one-to-one relationship between our two estimates of the number of YOY hatched in 1993–1995. The range was estimated using 95% CI around our adult and juvenile population estimates and the 95% CI around our YOY population estimates for late August.

[c]Cumulative number of YOY bass eaten by adult and juvenile largemouth bass by late August of each year. We estimated the range using 95% CI around our adult and juvenile population estimates.

[d]We estimated the range using the 95% CI around our adult and juvenile population estimates.

We detected significant declines in condition factor from fall to spring for both the 1993 (ANCOVA, $P < 0.05$) and 1994 cohorts ($P < 0.05$). Length-standardized mass of the 1993 and 1994 cohorts declined over winter by 0.12 and 0.06 g, respectively. The winter of 1993–1994 was longer than the winter of 1994–1995, which may help explain the greater mass loss for the 1993 cohort. The pattern of overwinter survival closely matched predictions derived from the Shuter et al. (1980) physiologically based, overwinter mortality model (Fig. 10).

The general relationship between overwinter survival and total length for Paul Lake bass was estimated using data from both the 1993 and 1994 cohorts (Fig. 11). The resulting sigmoidal relationship was

$$\text{relative survival} = \frac{\text{length}^{15}}{\text{length}^{15} + 54.5^{15}}$$

where relative survival was the percentage of fish surviving the winter and length was total length (mm) entering the winter. The parameter estimates and standard errors were $a = 15$ (3.9) and $b = 54.5$ (1.0). The standard error of estimates for this model was 0.97. This model indicates that the relative overwinter survival of 50 mm bass was 20%, while the relative survival of 60 mm bass was 80%.

Discussion

Our results indicate that adult demography, predation, and size-selective overwinter mortality act in series to regulate recruitment in Paul Lake. Furthermore, hatching date, predation, and growth rate interact to influence overwinter mortality. It is the complex hierarchical interaction of these processes that governs recruitment of largemouth bass in Paul Lake.

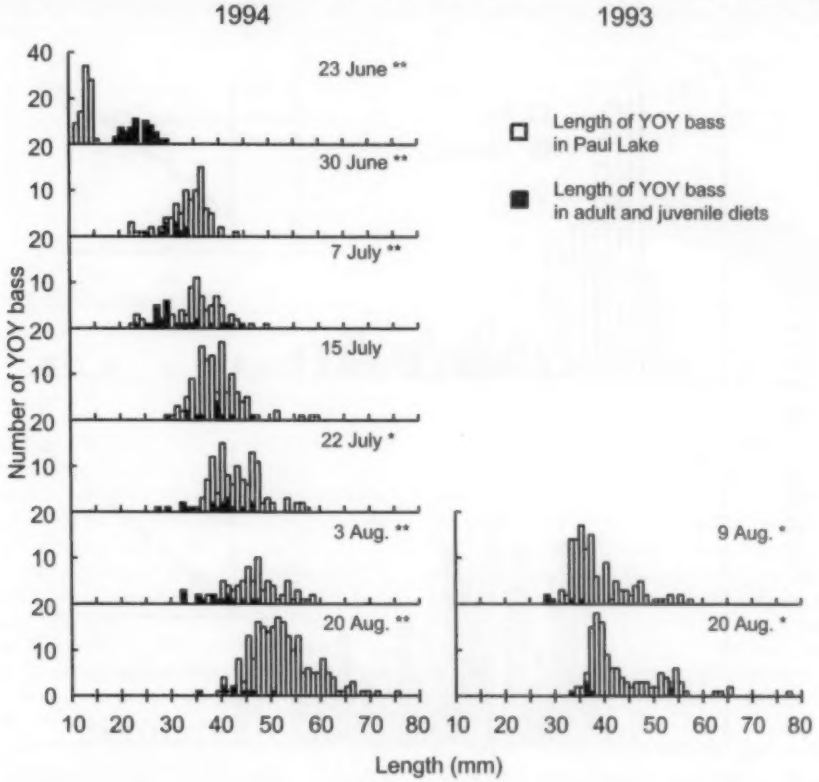
There is strong correlation between the spring density of reproductively mature adults and the number of YOY hatched but not between the number of YOY hatched and August YOY densities. This is consistent with previous studies (e.g., Elliott 1984; Sissenwine 1984) that report a positive correlation between the number of adults and the number of eggs spawned but no correlation between the number of eggs spawned and cohort abundance later in life. Thus, adult density and the number of eggs spawned are generally poor predictors of eventual year class size. In Paul Lake, the number of eggs spawned (and fish hatched) provides the backdrop for recruitment but by itself is not a good predictor of year-class strength.

Impact of inter-cohort cannibalism

The pattern of summer survival for a YOY cohort depends on the intensity of inter-cohort predation. In years of high adult and juvenile abundance, most YOY bass are eaten. In these years, adult and juvenile bass could have eaten many more YOY bass than were available (Table 2) and cannibalism was so intense that YOY bass would appear in adult and juvenile diets for only a few weeks of the summer. Thus, predation was limited by the number of YOY hatched. The few YOY bass that survive the summer are likely a conse-

© 1998 NRC Canada

Fig. 8. Evidence for size-selective predation by adult and juvenile largemouth bass in 1993 and 1994. Significant differences in the YOY size distributions from the lake and from adult and juvenile bass diets are indicated by * ($P < 0.05$) and ** ($P < 0.01$).



quence of the adult and juvenile diet response. As the abundance of a YOY largemouth bass cohort declines below a few hundred individuals, cannibalism by adults and juveniles declines. Reduced predation likely results from low encounter rates and (or) effective refuging behavior by YOY bass. In years of low adult and juvenile abundance, there are fewer predators, and although they prey on YOY throughout the summer, their impact on a cohort is less. In these years, more YOY bass survive the summer.

Although there is no absolute refuge in larger size for YOY bass in Paul Lake, cannibalism was strongly focused on the smaller members of each YOY cohort. In years with relatively low predation, the interaction of size-selective predation and relative spawning date were important for the survival of individual YOY bass. In 1994, YOY were subject to intense predation immediately after nest school dispersal. This corresponded with the cessation of nest school guarding behavior of adult male largemouth bass. YOY bass are guarded in nest schools by adult males until they reach about 15–20 mm in length (Brown 1985; personal observation), and male guarding limits predation during this period (Bain and Helfrich 1983). Early-spawned fish that survived the first few weeks after nest school dispersal and remained larger than average had a higher survival probability. However, many early-spawned fish did not maintain high growth rates and were, therefore, subject to cannibalism throughout the summer. In contrast, late-spawned individuals remained smaller than average and were vulnerable to predation throughout the entire summer. These patterns of size-selective predation should result in disproportionately high mortality rates for late-spawned fish. This pattern of mortality was confirmed by otolith analysis; late-spawned fish were underrepresented in the August sample (Table 1). We do not know which fish survive summers with high predation rates because the intense predation limits sample size. It is likely, however, that there is little or no age or size selection in these years because predation is intense and survival may be largely stochastic.

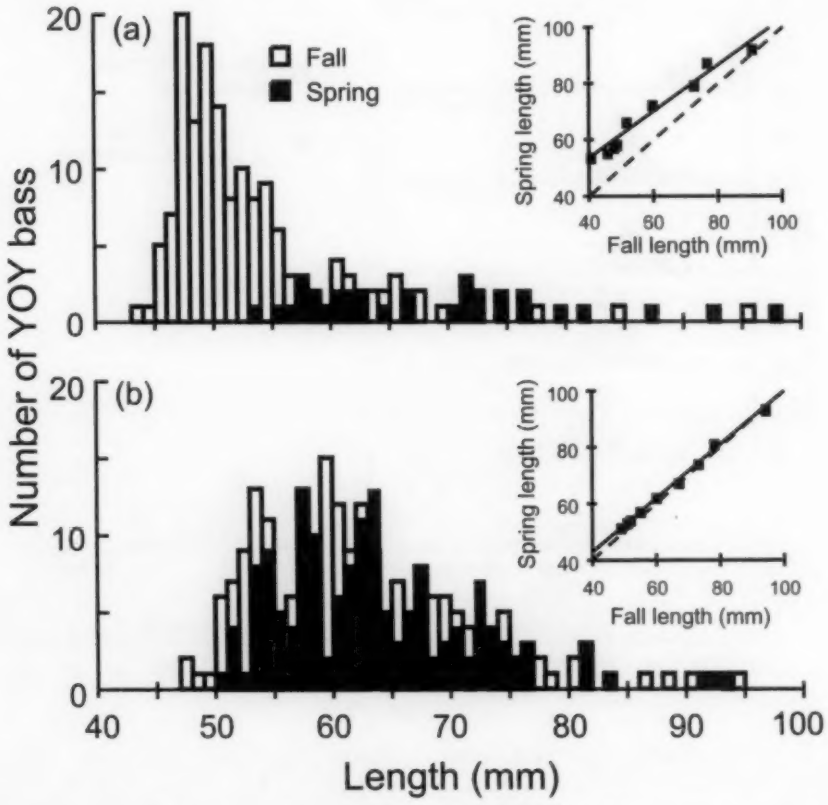
YOY largemouth bass in lakes with more complex fish communities may be subject to relatively low cannibalism because of the availability of alternative fish prey. Other studies have reported low occurrence of cannibalism in lakes with more complex fish communities (Timmons et al. 1980; Keast 1985). However, predation by other littoral predators (e.g., smallmouth bass, black crappie, bullheads, etc.; Keast 1985) may compensate for reduced cannibalism.

Growth rates and density

Density-dependent growth is widely reported among fish species (e.g., Peterman 1984; Bromley 1989) and can strongly impact fish survival and ultimate recruitment (e.g., Houde 1989). In Paul Lake, adult largemouth bass body condition was negatively correlated with adult densities (Schindler et al. 1997), indicating density-dependent growth.

© 1998 NRC Canada

Fig. 9. Length frequency distributions of the (*a*) 1993 and (*b*) 1994 YOY bass cohorts in late fall (October) and early spring (early May). Insets show quantile–quantile plots for the 1993 and 1994 cohorts. The broken line is the 1:1 relationship and the solid line is the least squares regression for each cohort. Points represent 1, 5, 10, 25, 50, 75, 90, 95, and 99% of the fall and spring length distributions.

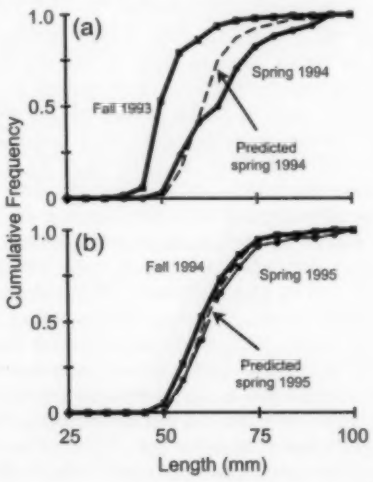


Although our sample size is small, the pattern of decreasing growth rates with increasing density is striking (Fig. 4) and is consistent with patterns of density-dependent growth of YOY bass shown experimentally in YOY bass (Olson et al. 1995) and many other species of fish. Furthermore, although temperature is an important factor governing growth (Kitchell et al. 1977; Rice et al. 1983), the observed pattern of growth rates was not consistent with interannual temperature patterns. Growth rates in 1993, a cold summer, were higher than growth rates in 1994, a relatively warm summer. Although not conclusive, our results suggest density-dependent growth of YOY largemouth bass in Paul Lake. The best fit relationship between density and growth rate (growth rate = 0.739–0.00005 · August density; $R^2 = 0.99$) indicates that for every 1000 fish·ha^{-1} increase in August densities, there should be a 7% decline in growth rates.

Overwinter mortality

Our results demonstrate that fish <50–60 mm do not survive the winter in Paul Lake. The length-dependent patterns of mortality, changes in condition factor overwinter, and predictions derived from the Shuter et al. (1980) overwinter mortality model are all similar to those from laboratory experiments on a variety of fishes (e.g., Oliver et al. 1979;

Fig. 10. Observed and predicted cumulative frequency curves for the (*a*) 1993 and (*b*) 1994 YOY bass cohorts. The predicted curve was generated from the physiologically based overwinter mortality model of Shuter et al. (1980) assuming a winter duration of 150 days in 1993 and 145 days in 1994.



© 1998 NRC Canada

Fig. 11. The relationship between relative overwinter survival probability and length entering the winter for the 1993 and 1994 largemouth bass cohorts. The size of each data point is proportional to its sample size and was used to weight the fitted relationship.

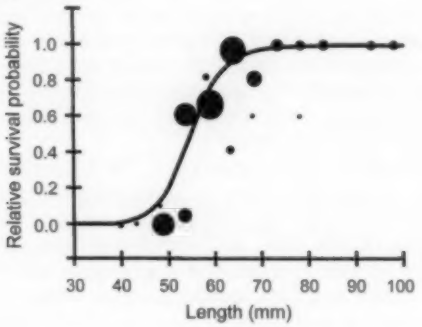
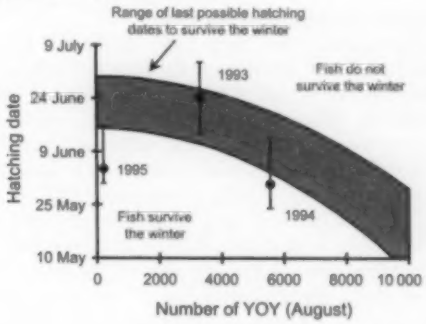


Fig. 12. Range of last possible hatching dates to survive the winter. Predicted conditions are from the observed patterns of density-dependent growth and assuming 100% mortality for fish <50–60 mm when entering the winter. The mean and range of hatching dates for the 1993–1995 cohorts are plotted against their respective August densities.



Post and Evans 1989) and strongly suggest that overwinter mortality was ultimately caused by starvation. This is consistent with the observation that overwinter mortality can strongly regulate recruitment in fish population near the northern limit of their range (Shuter and Post 1990).

Our result differs markedly from those of more southerly lakes and reservoirs where largemouth bass ≤90–100 mm are considered most susceptible to overwinter mortality (e.g., Toneys and Coble 1979; Miranda and Hubbard 1994*a*). These studies were all located at sites well south of the northern extent of the largemouth bass range, and all of them studied fish ≥60 mm in length. Latitudinal differences in overwinter mortality patterns may result from different proximate causes of mortality. Miranda and Hubbard (1994*b*) demonstrated that predation was the proximate source of size-dependent overwinter mortality in southern largemouth bass populations. Smaller fish suffered higher overwinter mortality in ponds with predators present than in ponds with no predators. In the absence of predators, Miranda and Hubbard (1994*b*) observed little size-dependent overwinter mortality. Their results, however, did not discount the possibility that starvation may increase susceptibility to predation. In lakes located at or near the northern extent of the largemouth bass range, starvation is probably most important. Largemouth bass of any size generally feed little at water temperatures <10°C (Johnson and Charlton 1960; Coutant 1975). Our fall and spring sampling occurred after temperatures had fallen below 10°C and just after temperatures had reached 10–12°C. Thus, the high overwinter mortality that we observed was not likely the result of predation. We can not, however, rule out the possibility that starvation increased the vulnerability of smaller YOY to predation and that predation was the proximate cause of death.

Spawning date, growth rate, and winter duration interact strongly to determine overwinter mortality. Although hatching date and winter duration are density independent, growth rate is inversely related to density. Furthermore, the intensity of cannibalism regulates August densities. Thus, the average length for members of a cohort entering the winter is indirectly affected by the intensity of cannibalism. We calculated a range of last possible hatching dates (LPHD) required to survive the winter across a range of YOY largemouth bass densities based on the observed pattern of growth (Fig. 4). We assumed that fish must reach 50 to 60 mm in length to survive the winter, that growth from hatching until late August was inversely related to density, and that individuals grow 8 mm from late August until winter (average growth rate from late August until winter for the 1993 and 1994 cohorts). As YOY largemouth bass density increases, the LPHD becomes progressively earlier (Fig. 12). Over the range of observed August abundance (from 0 to about 6000), the LPHD recedes by nearly 20 days.

Winter duration varies from year to year and affects the LPHD by changing the minimum size required to survive the winter (Shuter et al. 1980). For example, as winter duration increases, the minimum size required to survive the winter increases. This shifts the LPHD isocline down, requiring earlier spawning or faster growth for overwinter survival. In contrast, a decrease in winter duration might permit a longer spawning season and the survival of later-spawned and slower-growing fish. A decrease in winter duration would also minimize the effects of density-dependent growth. Even at high densities (and slow growth), the longer growing season and shorter winter would allow better overwinter survival.

These observations are similar to those generated for smallmouth bass by DeAngelis et al. (1991) using an individual-based model. Overwinter mortality is not independent of summer mortality because of the density-dependent growth response. Thus, increased predation can increase growth rates, which may, depending on the hatching date, increase the probability of overwinter survival.

Although we can predict the general patterns of cohort survival, individual survival is harder to predict. If size and age were strongly correlated, then LPHD would predict which individuals survive the winter based on hatching date alone. However, in Paul Lake, age accounts for ≤40% of the observed variability in size. Late-spawned individuals were generally smaller than early-spawned individuals and were, therefore, more vulnerable to overwinter mortality. However, the growth rates of early-spawned individuals were variable, and many early-hatched fish enter the winter <55 mm

© 1998 NRC Canada

(equivalent to <47 mm in late August, assuming 8 mm of growth between late August and winter; Fig. 6). Although overwinter mortality was generally highest for late-spawned individuals, it was also a substantial source of mortality for early-hatched, slow-growing individuals.

Hierarchical process of recruitment

Our observations allow us to make qualitative predictions about the patterns of recruitment for largemouth bass in Paul Lake. The number of adults provides the ultimate constraint on recruitment. When the number of adults is low, recruitment will be low regardless of other processes. Furthermore, if the number of predators (adult and juvenile bass, but predominately juveniles) is high, recruitment will be low regardless of adult densities and overwinter mortality. If the number of adults is moderate to high and predation is low, then recruitment through the first year of life depends on the number of adults and the interaction of overwinter mortality, hatching date, and summer growth rates. If the hatching date is early, the growing season is long enough to allow high overwinter survival, except at exceptionally high YOY densities, and the number of YOY surviving the first year of life depends on the number of mature adults. When hatching date is late, however, overwinter mortality becomes more important.

Of the multiple pathways possible, only one allows high recruitment through the first year of life. There must be a relatively large number of adults, low density of predators, and early spawning to allow good overwinter survival. A large number of adults with a low density of predators only occurs when there are few juvenile bass present. All other scenarios result in low recruitment. From 1992 through 1995, we observed four of the possible scenarios. In 1992, the number of adults was very low and recruitment was negligible. In 1993 and 1994, there were a moderate to high number of adult bass and predation was low, but the 1993 cohort was hatched late and therefore suffered high overwinter mortality. The 1994 cohort was hatched early, despite slow growth rates, and had relatively low overwinter mortality, and first year survival was high. In 1995, there were a lot of adult bass and the cohort hatched early, but the density of predators was very high (because of the large 1994 cohort) and summer survival was poor.

Population dynamics and food web structure

YOY largemouth bass are the only important vertebrate zooplanktivore in Paul Lake and can have a large impact on the pelagic food web when abundant (Post et al. 1997). Thus, pelagic food web dynamics are closely linked to largemouth bass population dynamics through recruitment.

The intense cannibalism produces two alternate population states in Paul Lake: high or low adult and juvenile densities. The high density state may be initiated by a large recruitment event such as the 1994 cohort. A large cohort increases predation pressure and maintains high reproductive potential over its effective life span. The high predation potential will suppress subsequent strong recruitment events. If predation eliminates entire cohorts, then predation pressure will decrease as the cohort ages and irruptive recruitment events will occur at a periodicity near that of the life span of a cohort (Carpenter 1988). However, because a few YOY bass survive each year in Paul Lake, high predation pressure will be maintained past the effective cohort life span. The length of the high density period is a function of the ratio of recruitment and adult mortality (R/M). If $R/M = 1$, the population will remain stable until externally perturbed. As R/M approaches 0, the length of high density periods approaches the effective cohort life span. Factors that would move Paul Lake from high to low adult and juvenile densities include a series of reproductive failures (like those observed in acidified lakes), partial winter-kill events, increased fishing pressure, and cohort senescence.

The alternative state in Paul Lake, low adult and juvenile densities, is transient. At low densities, irruptive recruitment events (like we observed in 1994) move the population back to the high density state. Although low density states may persist for >1 year as a result of density-independent reproductive failure (e.g., no spawning, nest abandonment, or high overwinter mortality), consecutive large recruitment events should be rare. A large cohort that survives both the summer and winter will re-establish the high juvenile density in its second summer. That is what occurred in 1995 when the 1994 cohort recruited into the juvenile population and, through cannibalism, helped suppress the 1995 cohort. By the fall of 1996, the large 1994 cohort represented over 80% of the adult and juvenile largemouth bass population.

At high adult and juvenile densities, Paul Lake is a piscivore-dominated system. There are few small planktivorous fishes (Carpenter and Kitchell 1993) and benthic invertebrates serve as alternative prey, which maintains high adult and juvenile biomass (Carpenter and Kitchell 1993; Schindler et al. 1997). However, small fish (including YOY largemouth bass) are the preferred and optimal prey for largemouth bass (Hodgson and Kitchell 1987). The high potential for piscivory (maintained by benthic foraging) and preference for small fishes buffers Paul Lake from invasions by planktivorous fishes (including YOY largemouth bass) and maintains piscivore dominance. Any breakdown in piscivore dominance will be transient. The pulse of planktivory caused by a large cohort of YOY largemouth bass will usually be short lived (Post et al. 1997). As the cohort matures and switches from zooplanktivory to benthivory and piscivory, its role in the food web reverses and piscivore dominance is re-established (Post et al. 1997). Because largemouth bass dominate the Paul Lake fish community, largemouth bass population dynamics, fish community structure, and pelagic food web structure are all tightly coupled.

Acknowledgments

We thank T. Essington, B.R. Herwig, J.M. Johnson, J. Knetter, and D.E. Schindler for assistance in the laboratory and in the field. We also thank all past members of the Cascade Project fish team, especially X. He and R.A. Wright, and all technicians and students who worked with J.R. Hodgson over the years. We thank J.J. Isely at Clemson University and members of the otolith analysis lab at the University of North Carolina State for teaching DMP otolith analysis techniques. Comments by S.R. Carpenter, A.R. Ives, T.B. Johnson, L.M. Puth, and two anonymous referees improved this manuscript. This work was facilitated by M. Berg, R. Hellenthal, J. Runde, and T. Frost. This research

© 1998 NRC Canada

was supported by grants from the Ecosystem Program, National Science Foundation, to JFK and fellowship support to DMP from the Electric Power Research Institute.

References

Bain, M.B., and Helfrich, L.A. 1983. Role of male parental care in survival of larval bluegills. Trans. Am. Fish. Soc. **112**: 47–52.

Bromley, P.J. 1989. Evidence for density-dependent growth in North Sea gadoids. J. Fish Biol. **35**(Suppl. A): 117–123.

Brown, J.A. 1985. The adaptive significance of behavioural ontogeny in some centrarchid fishes. Environ. Biol. Fishes, **13**: 25–34.

Carpenter, S.R. 1988. Transmission of variance through lake food webs. *In* Complex interactions in lake communities. *Edited by* S.R. Carpenter. Springer-Verlag, New York. pp. 119–138.

Carpenter, S.R., and Kitchell, J.F. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, England.

Clutton-Brock, M. 1967. Likelihood distributions for estimating functions when both variables are subject to errors. Technometrics, **9**: 261–269.

Coutant, C.C. 1975. Responses of bass to natural and artificial temperature regimes. *In* Black bass biology and management. *Edited by* H. Clepper. Sport Fishing Institute, Washington, D.C. pp. 272–285.

Crowder, L.B., Rice, J.A., Miller, T.J., and Marschall, E.A. 1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. *In* Individual-based approaches in ecology: concepts and individual models. *Edited by* D. DeAngelis and L. Gross. Routledge, Chapman and Hall, New York. pp. 237–255.

DeAngelis, D.L., Godbout, L., and Shuter, B.J. 1991. An individual-based approach for predicting density-dependent dynamics in smallmouth bass populations. Ecol. Model. **57**: 91–115.

Draper, N.R., and Smith, H. 1981. Applied regression analysis. 2nd ed. Wiley, New York.

Efron, B., and Tibshirani, R.J. 1993. An introduction to the bootstrap. Chapman and Hall, New York.

Elliott, J.M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a lake district stream, 1966–83. J. Anim. Ecol. **53**: 327–350.

Fogarty, M.J., Sissenwine, M.P., and Cohen, E.B. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends Ecol. Evol. **6**: 241–246.

Forney, J.L. 1977. Reconstruction of yellow perch (*Perca flavescens*) cohorts from examination of walleye (*Stizostedion vitreum vitreum*) stomachs. J. Fish. Res. Board Can. **34**: 925–932.

Hewett, S.W., and Johnson, B.J. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute. Technical Report WIS-SG-92-250, Madison, Wis.

Hodgson, J.R., and Kitchell, J.F. 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides*). Am. Midl. Nat. **118**: 323–336.

Hodgson, J.R., and Cochran, P.A. 1988. The effect of sample methodology on diet analysis in largemouth bass (*Micropterus salmoides*). Verh. Int. Ver. Limnol. **23**: 1670–1675.

Hodgson, J.R., Carpenter, S.R., and Gripentrog, A.P. 1989. Effects of sampling frequency on intersample variance and food consumption estimates of nonpiscivorous largemouth bass. Trans. Am. Fish. Soc. **118**: 11–19.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Sym. **2**: 17–29.

Houde, E.D. 1989. Subtleties and episodes in the early life of fishes. J. Fish Biol. **35**(Suppl. A): 29–38.

Isley, J.J., and Nobel, R.L. 1987. Validation of daily ring deposition in otoliths of wild young-of-the-year largemouth bass. Tex. J. Sci. **39**: 273–277.

Johnson, M.G., and Charlton, W.H. 1960. Some effects of temperature on the metabolism and activity of the largemouth bass, *Micropterus salmoides* Lacepéde. Prog. Fish-Cult. **22**: 155–163.

Keast, A. 1985. The piscivorous feeding guild of fishes in small freshwater ecosystems. Environ. Biol. Fishes, **12**: 119–129.

Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1922–1935.

Krebs, C.J. 1989. Ecological methodology. Harper and Row, New York.

Lawrence, J.M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. **11**(1957): 220–225.

Leavitt, P.R., Carpenter, S.R., and Kitchell, J.F. 1989. Whole-lake experiments: the annual record of fossil pigments and zooplankton. Limnol. Oceanogr. **34**: 700–717.

Luecke, C., Rice, J.A., Crowder, L.B., Yeo, S.E., and Binkowski, F.P. 1990. Recruitment mechanisms of bloater in Lake Michigan: an analysis of the predatory gauntlet. Can. J. Fish. Aquat. Sci. **47**: 524–532.

Miller, S.J., and Storck, T. 1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. Trans. Am. Fish. Soc. **111**: 527–530.

Miller, S.J., and Storck, T. 1984. Temporal spawning distribution of largemouth bass and young-of-year growth, determined from daily otolith rings. Trans. Am. Fish. Soc. **113**: 571–578.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**: 1657–1670.

Miranda, L.E., and Hubbard, W.D. 1994*a*. Length-dependent winter survival and lipid composition of YOY largemouth bass in Bay Spring Reservoir, Mississippi. Trans. Am. Fish. Soc. **123**: 80–87.

Miranda, L.E., and Hubbard, W.D. 1994*b*. Winter survival of YOY largemouth bass relative to size, predators, and shelter. N. Am. J. Fish. Manag. **14**: 790–796.

Oliver, J.D., Holeton, G.F., and Chua, K.E. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Trans. Am. Fish. Soc. **108**: 130–136.

Olson, M.H., Mittelbach, G.G., and Osenberg, C.W. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology, **76**: 1758–1771.

Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **41**: 1825–1829.

Post, J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. **46**: 1958–1968.

Post, D.M., Carpenter, S.R., Christensen, D.L., Cottingham, K.L., Kitchell, J.F., Schindler, D.E., and Hodgson, J.R. 1997. Seasonal effects of variable recruitment of a dominant piscivore on pelagic food web structure. Limnol. Oceanogr. **42**: 722–729.

Reilly, P.M., and Patino-Leal, H. 1981. A bayesian study of the error-in-variables model. Technometrics, **23**: 221–231.

Rice, J.A., and Cochran, P.A. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology, **65**: 732–739.

© 1998 NRC Canada

Rice, J.A., Breck, J.E., Bartell, S.M., and Kitchell, J.F. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ. Biol. Fishes, **9**: 263–275.

SAS Institute, Inc. 1985. SAS user's guide: statistics. 5th ed. SAS Institute, Cary, North Carolina, U.S.A.

Schindler, D.E., Hodgson, J.R., and Kitchell, J.F. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia, **110**: 592–600.

Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. No. 184, Ottawa, Canada.

Shuter, B.J., and Post, J.R. 1990. Climate, population viability, and the zoogeography of temperate fishes. Trans. Am. Fish. Soc. **119**: 314–336.

Shuter, B.J., MacLean, J.A., Fry, F.E.J., and Regier, H.A. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. Fish. Soc. **109**: 1–34.

Sissenwine, M.P. 1984. Why do fish populations vary? *In* Exploitation of marine communities. *Edited by* R. M. May. Springer-Verlag, New York. pp. 59–94.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. 2nd ed. W.H. Freeman and Company, New York.

Summerfelt, R.C. 1975. Relationship between weather and year-class strength of largemouth bass. *In* Black bass biology and management. *Edited by* R. Clepper. Sport Fishing Institute, Washington, D.C. pp. 166–174.

Timmons, T.J., Shelton, W.L., and Davies, W.D. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama–Georgia. Trans. Am. Fish. Soc. **109**: 176–186.

Toneys, M.L., and Coble, D.W. 1979. Size-related, first winter mortality of freshwater fishes. Trans. Am. Fish. Soc. **108**: 415–419.

Trebitz, A.S. 1991. Timing of spawning in largemouth bass: implications of an individual-based model. Ecol. Model. **59**: 203–227.

Whitledge, G.W., and Hayward, R.S. 1997. Laboratory evaluation of a bioenergetics model for largemouth bass at two temperatures and feeding levels. Trans. Am. Fish. Soc. **126**: 1030–1035.

© 1998 NRC Canada

Stable carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*)

Keith A. Hobson and Don M. Schell

Abstract: Previous measurements of naturally occurring stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) along the baleen plates of western Arctic bowhead whales (*Balaena mysticetus*) have provided a continuous lifetime record of the feeding or nutritional ecology of these animals that migrate annually between isotopically different foodwebs. However, virtually nothing was known about isotopic patterns of eastern Arctic bowheads. We measured $\delta^{13}C$ and $\delta^{15}N$ values along the baleen plates of three eastern and one western Arctic bowhead whales taken from Canadian waters in 1988 and 1996. In contrast to western Arctic animals, we found strong evidence for periodic fluctuations in $\delta^{15}N$ but not $\delta^{13}C$ values in the eastern Arctic specimens. We interpret these results as evidence that eastern Arctic animals do not move between foodwebs that differ in $\delta^{13}C$ signature and suggest that these whales either (*i*) move annually between areas isotopically enriched in ^{15}N but not ^{13}C, (*ii*) shift diet annually by about one third of a trophic level, or (*iii*) undergo seasonal fasting that results in enrichment of baleen $\delta^{15}N$ resulting from protein catabolism.

Résumé : Les mesures effectuées sur l'occurrence naturelle des isotopes stables du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) le long des fanons de baleines boréales (*Balaena mysticetus*) de l'Arctique occidental ont fourni un témoignage suivi, couvrant la vie entière, de l'écologie alimentaire ou nutritionnelle de ces animaux qui migrent chaque année entre des réseaux trophiques isotopiquement différents. Toutefois, on ne savait pratiquement rien des patrons isotopiques des baleines boréales de l'Arctique oriental. Nous avons mesuré les valeurs de $\delta^{13}C$ et de $\delta^{15}N$ le long des fanons de trois spécimens de l'Est et d'un spécimen de l'Ouest capturés dans les eaux canadiennes en 1988 et 1996. Par rapport aux baleines de l'Arctique occidental, nous avons trouvé de fortes indications de fluctuations périodiques du $\delta^{15}N$ mais pas du $\delta^{13}C$ aux spécimens de l'Artique oriental. Nous voyons dans ces résultats la preuve que les animaux de l'Arctique oriental ne se déplacent pas entre des réseaux trophiques qui diffèrent sur le plan de la signature de $\delta^{13}C$, et nous pensons que ces baleines (*i*) soit se déplacent chaque année entre des zones enrichies en isotopes de ^{15}N mais non de ^{13}C, (*ii*) soit modifient chaque année leur régime alimentaire d'environ un tiers de niveau trophique, (*iii*) soit subissent un jeûne saisonnier qui occasionne un enrichissement en $\delta^{15}N$ dû au catabolisme des protéines.

[Traduit par la Rédaction]

Introduction

Two distinct populations of bowhead whales (*Balaena mysticetus*) are recognized and occur primarily in the arctic waters of eastern and western North America, respectively (Moore and Reeves 1993). The western Arctic population consists of approximately 5 000 – 10 000 individuals that migrate annually between the eastern Beaufort Sea and the Mackenzie Delta in summer and the Chukchi and northern Bering Sea in winter (Schell et al. 1989*a*, 1989*b*; Moore and Reeves 1993). In contrast, the eastern Arctic population consists of perhaps 700 individuals and occurs in waters of Northern Hudson Bay, eastern Lancaster Sound and Baffin Bay. Less is known about the ecology and annual movements of these individuals (Zeh et al. 1993) although whales in Davis Strait and Hudson Bay are thought to be separate stocks (see also Cosens et al. 1997).

The high-latitude distribution of bowhead whales has undoubtedly contributed to our lack of basic knowledge of the ecology and natural history of this species. Recently, Schell and Saupe (1993) used stable isotope analysis of the baleen and other tissues of western Arctic bowheads to investigate feeding and growth. They determined that the stable carbon and nitrogen isotopic ratios in baleen varied in a regular pattern down the length of the baleen and postulated that this variation reflected the annual movements of whales between relatively isotopically depleted food sources of the eastern portion of the summer range to the more enriched diets in the Bering and Chukchi seas (see also Schell et al. 1989*a*, 1989*b*). The baleen was thus interpreted to provide a continuous isotopic record that could not only reveal annual changes in diet but could also supply important information on the minimum age of individuals. This approach has provided a critical tool in assessing basic reproductive parameters in and management of this whale stock (Schell and Saupe 1993).

Received April 6, 1998. Accepted September 11, 1998.
J14550

K.A. Hobson.[1] Prairie and Northern Wildlife Research Centre, 115 Perimeter Road, Saskatoon, SK S7N 0X4, Canada,
D.M. Schell. Institute of Marine Science, University of Alaska, Fairbanks, AK 99775-5220, U.S.A.

[1]Author to whom all correspondence should be addressed. Present address: Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, SK S7N 0X4, Canada.
e-mail: keith.hobson@ec.gc.ca

© 1998 NRC Canada

Table 1. Collection data for three eastern Arctic and one western Arctic bowhead whales whose baleen plates were measured along their lengths for $\delta^{13}C$ and $\delta^{15}N$ values.

Sample	Date	Location	Cause of death	Sex	Length (m)	Length of baleen (m)	Minimum age (years)
Eastern Arctic							
96-02	18/08/96	Repulse Bay, N.W.T.	Licenced hunt	Male	14.90	2.84	20
96-03	2/08/96	Cape Dorset, N.W.T.	Unknown	Female	8.87	nd	8?
88-01	1988	Cumberland Sound, N.W.T.	Unknown	Unknown	nd	>2.9	20
Western Arctic							
96-01	24/07/96	Shingle Point, Yukon	Licensed hunt	Male	11.20	2.05	10

Note: Minimum ages are derived from counting isotopic oscillations along the baleen plates and do not account for the unknown amount of wear that has occured on the tips. Date expressed as day/month/year. nd, no data available.

The use of stable-isotope analysis to investigate the ecology of western Arctic bowhead whales is based on the assumption that isotope ratios in the baleen largely reflect the diet of the animal during its formation. Schell and Saupe (1993) postulated that geographic variation in stable carbon isotope signatures of prey zooplankton observed between wintering and summering areas (Dunton et al. 1989) causes oscillations in the carbon isotope signature along the length of the baleen of animals moving between these areas. This hypothesis was supported by the fact that whales killed in the fall in the eastern Beaufort Sea showed ^{13}C-depleted baleen being formed, whereas those killed during the spring northward migration showed ^{13}C-enrichment in the newest formed baleen. Support for annual oscillations in isotope signatures of the western arctic bowhead whale baleen was also provided by radioacarbon measurements that showed an increase in ^{14}C corresponding to a period of atmospheric bomb tests in the early 1960s (Schell et al. 1989*b*). Oscillations of stable nitrogen isotope ratios along the baleen are harder to interpret since ^{15}N enrichment can be caused by changes in foodweb isotopic signature (Michener and Schell 1994; Schell et al. 1998), trophic level (Fry 1988; Hobson and Welch 1992) and also by fasting or nutritional stress (Hobson et al. 1993).

As a result of the low population of eastern Arctic bowhead whales, subsistence hunting of this population has been restricted since 1979 and so few specimens have been available for scientific investigation. However, the recent authorization of the hunt of a few individuals by local Inuit hunters combined with the salvage of material from two animals found dead has allowed the isotopic investigation of three eastern Arctic bowheads and a single western Arctic bowhead from Canadian waters. The objective of this study was to examine the baleen of eastern Arctic bowheads in order to see if the regular patterns of stable carbon and nitrogen isotopic variation along the length of baleen seen in western Arctic populations also occur in the eastern populations. If no pattern was found, this result would strengthen the current interpretation by Schell and coworkers that such variation in western Arctic whales clearly reflected the movement of those whales between two isotopically distinct foodwebs. On the other hand, the presence of a regular isotopic pattern in eastern Arctic bowheads would suggest that such variation might be linked with other, perhaps physiological factors such as annual fasting, or indeed that eastern Arctic animals also move seasonally between foodwebs that differ regularly in their isotopic composition.

Methods

Sampling

Single baleen plates from three bowhead whales were obtained from the Department of Fisheries and Oceans (DFO) at the Freshwater Institute, Winnipeg, Man. (Table 1). The largest plate (96-02) was from a 14.9-m male bowhead taken during a licensed hunt by Inuit hunters in the vicinity of Repulse Bay, Northwest Territories, in 1996. A smaller plate (96-03) was from an 8.9-m female found at Cape Dorset, Northwest Territories, also in 1996. The single western Arctic sample (96-01) was from an 11.1-m male bowhead killed legally by Inuit hunters in the vicinity of Shingle Point, Yukon, near the Mackenzie Delta. Our eastern Arctic sample was further augmented by sampling of a plate recovered from a dead stranded whale in Cumberland Sound in 1988 (88-01).

Laboratory techniques

Before sampling, the baleen was cleaned of surface oils and adhered material using steel wool and a 2:1 chloroform:methanol solvent. Following the methods of Schell and Saupe (1993), baleen was sampled at 2.5-cm intervals along the outside edge with an engraving tool and the powdered baleen was used for isotopic analysis. Powdered baleen was loaded into tin cups and combusted in a Robo-Prep elemental analyzer at 1800°C. The resultant gases were separated and analyzed in a Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS) for stable carbon and nitrogen isotope ratios on the same sample. CFIRMS involves the automated sequential measurement of samples (unknowns) together with reference material. We used two laboratory standards (egg albumen) for every five unknowns in sequence. Stable-isotope ratios were expressed in δ notation as parts per thousand deviation from the international standards PDB (carbon) and AIR (nitrogen) (see Schell and Saupe 1993). We also compared analytical precision corresponding to analyses run at the Department of Soil Science, University of Saskatchewan, Saskatoon (K.A.H.) with that at the Institute of Marine Science, University of Alaska, Fairbanks (D.M.S.), and, using a baleen standard provided from the latter laboratory, determined that the results from the former laboratory were comparable with the latter at the level of ±0.3‰ for nitrogen and ±0.2‰ for carbon. We are thus confident that the isotope data presented here are consistent within our sample and can further be compared directly with those reported by Schell et al. (1989*a*, 1989*b*).

We compared mean stable-isotope composition of baleen plates using analysis of variance (ANOVA). When significant differences were detected ($p < 0.05$), we used a Tukey's multiple comparison test to examine differences between individuals. The relationship between baleen $\delta^{15}N$ and $\delta^{13}C$ values within plates was examined using linear regression. All statistical analyses were performed using SPSS for Windows, version 6.1.

© 1998 NRC Canada

Results

For two of the three eastern Arctic bowhead whales, we determined periodic fluctuations in $\delta^{15}N$ values but not in $\delta^{13}C$ values along the length of their baleen plates (Figs. 1*a* and 1*c*). The other eastern Arctic animal (Fig. 1*b*) showed less regular oscillations in $\delta^{15}N$ but also no oscillations in $\delta^{13}C$ values. This was in contrast with the expected periodic fluctuations in both $\delta^{15}N$ and $\delta^{13}C$ that we found for the single western Arctic animal (Fig. 1*d*). These results were also presented graphically by plotting $\delta^{15}N$ and $\delta^{13}C$ for eastern Arctic bowheads and the single western Arctic bowhead. The lack of a correlation between $\delta^{15}N$ and $\delta^{13}C$ values for eastern Arctic bowheads resulted in clouds of data (Fig. 2) compared with the more linear relationship found for the western Arctic bowhead (Fig. 3).

Within the eastern Arctic sample, we found isotopic variation among individuals (Table 2, Fig. 2). All animals differed in their overall mean $\delta^{15}N$ values (ANOVA, $F_{2,260} = 393.7$, $p < 0.0001$; Tukey's, $p < 0.05$ for all comparisons), but the youngest animal (96-03) was substantially more enriched in ^{15}N than the other two. Similarly, mean $\delta^{15}N$ maxima ($F_{2,40} = 464.1$, $p < 0.0001$) and minima ($F_{2,42} = 93.4$, $p < 0.0001$) values differed among these three individuals. The mean $\delta^{13}C$ baleen values also differed among eastern Arctic individuals ($F_{2,262} = 18.7$, $p < 0.0001$) but here only whale 96-02 was significantly more enriched than the other two (Tukey's, $p < 0.05$; Fig. 2).

The single western Arctic bowhead was more depleted in ^{13}C compared with the three eastern Arctic whales ($F_{3,332} = 342.9$, $p < 0.0001$; Tukey's, $p < 0.05$). However, the mean $\delta^{15}N$ value for this animal was indistinguishable from that of the younger eastern Arctic animal (Tukey's, $p > 0.05$).

Discussion

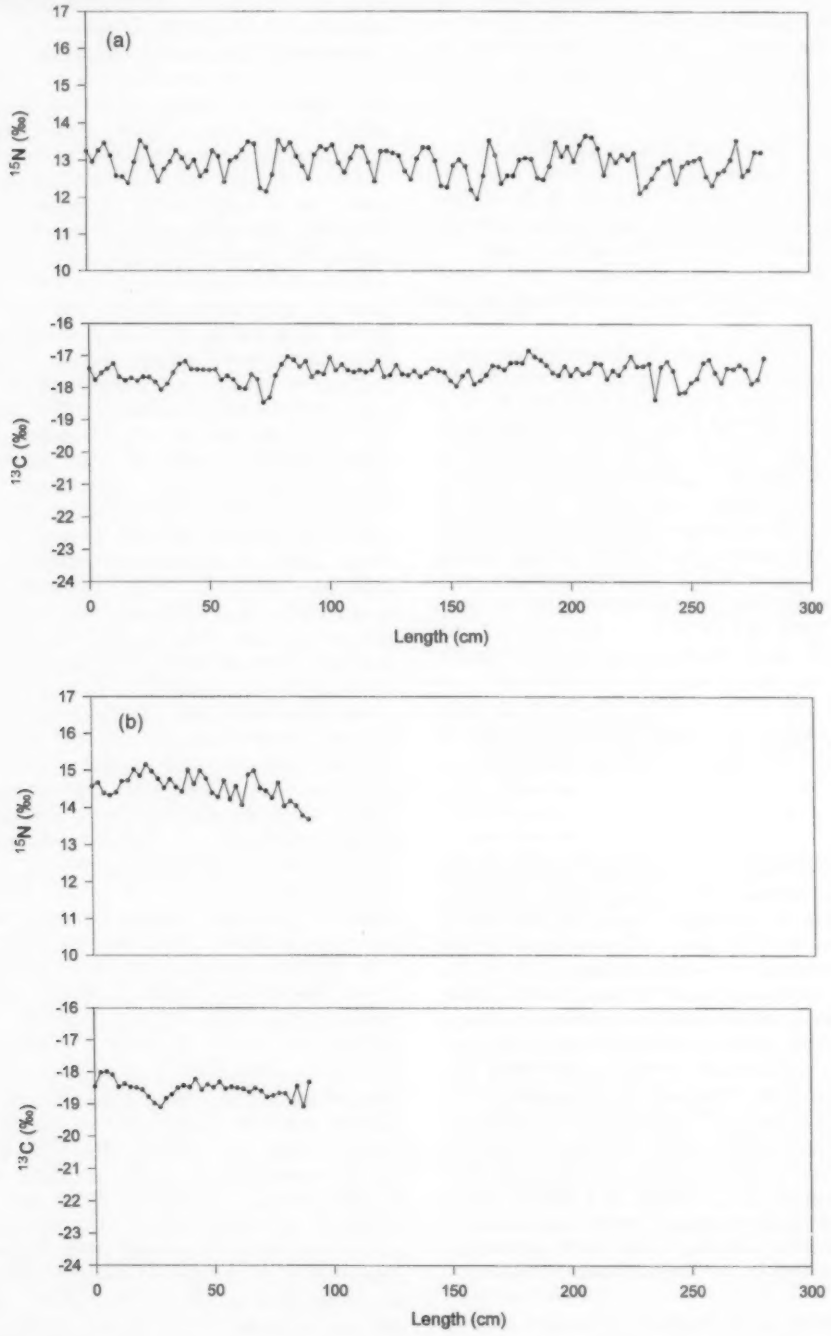
Two of the three eastern Arctic bowhead whales showed distinct periodic oscillations in $\delta^{15}N$ values along the length of their baleen plates but all eastern Arctic whales showed no regular oscillation in $\delta^{13}C$ values. This contrasts with the distinct periodic fluctuations in both isotopes recorded for the single western Arctic individual measured in this study and with the numerous individuals measured by Schell and Saupe (1993) for other western Arctic bowheads. We consider three possible explanations for our results. First, it is possible that eastern Arctic bowheads move seasonally between foodwebs that differ in $\delta^{15}N$ but not in $\delta^{13}C$ signature. Secondly, these whales might switch the trophic level of their prey seasonally, an effect influencing primarily $\delta^{15}N$ but not $\delta^{13}C$ signatures (e.g., Hobson and Welch 1992). Finally, whales may undergo regular fasting that results in enrichment of tissue ^{15}N, including that in newly formed baleen, during the fast. Below, we consider each of these possibilities in turn.

Schell and coworkers have conducted extensive isotopic measurements of the foodwebs used by western Arctic bowhead whales (Schell et al. 1989*a*, 1989*b*, 1998) and have demonstrated clearly that these animals move between an isotopically enriched foodweb in the western Chukchi and Beaufort Seas compared with a relatively depleted foodweb in the region of the Mackenzie Delta. Unfortunately, few data are available for the eastern Arctic (but see Hobson and Welch 1992), and we are aware of no isotopic foodweb data from northern Hudson Bay or Davis Strait where bowheads are known to congregate (Cosens et al. 1997). D.M. Schell (unpublished data) has demonstrated a negative cline in zooplankton $\delta^{13}C$ signatures from the western Arctic to Lancaster Sound in the vicinity of Resolute Bay, N.W.T. (74°42′N, 94°54′W) and K.A. Hobson (unpublished data) measured mysid and small amphipod $\delta^{13}C$ and $\delta^{15}N$ values to average -18.0 ± 1.4‰ and 8.8‰ ($n = 8$ composite samples), respectively, for Coburg Island, Northwest Territories (75°50′N, 79°25′W). The Coburg Island samples have relatively enriched $\delta^{13}C$ values but depleted $\delta^{15}N$ values compared with western Arctic samples. However, these samples may not be directly comparable with the western Arctic sample of Schell et al. (1998) since they were collected inshore and lipids were removed prior to analysis. Pelagic foodwebs tend to be more depleted in ^{13}C compared with inshore or benthically linked foodwebs (France 1995), and lipids are generally more depleted in ^{13}C compared with other tissues (Parker 1962). Currently, the mechanisms influencing isotopic signatures of marine foodwebs via primary production have received considerable attention. The effects of cellular growth rates on isotope ratios have been described by Laws et al. (1995) for laboratory cultures of a diatom and for haptophytes in the laboratory and world oceans by Bidigare et al. (1997). In general, conditions of rapid phytoplankton cell growth rates result in lowered isotopic discrimination during fixation and more enriched nitrogen and carbon isotopic signatures in primary producers. Other factors, such as water temperature and concentrations of dissolved carbon dioxide, are also known to influence carbon isotope ratios of marine particulate organic carbon (POC) (Wong and Sackett 1978; Rau et al. 1996). Enriched particulate organic nitrogen (PON) values are often associated with regions of upwelling (Altabet and McCarthy 1985). Animals moving regularly between waters rich in nutrients and those depleted in nutrients might show oscillations in isotope signatures along the length of their baleen plates. However, we currently do not know enough about the distribution of isotopic signatures in $\delta^{15}N$ foodwebs in the eastern Arctic, particularly in those regions inhabited by bowhead whales, and whether or not whales could move between foodwebs in areas differing substantially in $\delta^{15}N$ but not in $\delta^{13}C$ signatures.

The two adult eastern Arctic bowheads showed annual fluctuations in $\delta^{15}N$ values of the order of 1‰ and the single juvenile possibly of 0.7‰. These amplitudes are considerably less than that found for the single western Arctic animal measured here (i.e., 1.9‰) or those values reported for a larger sample of western Arctic animals measured by Schell et al. (1989*a*, 1989*b*). Nevertheless, this represents about one third of a trophic shift assuming a diet–tissue trophic enrichment factor of about 3‰ (Fry 1988; Hobson et al. 1996). Such a shift in baleen $\delta^{15}N$ values could be explained by changes in the relative proportions of copepods, euphausiids, amphipods, or other higher trophic-level prey in the diet of whales on a seasonal basis (see foodweb isotope values reported in Hobson and Welch (1992)). Previous dietary studies of bowheads have shown that copepods euphausiids, mysids, and amphipods comprise most of the diet of these animals (Lowry 1993).

© 1998 NRC Canada

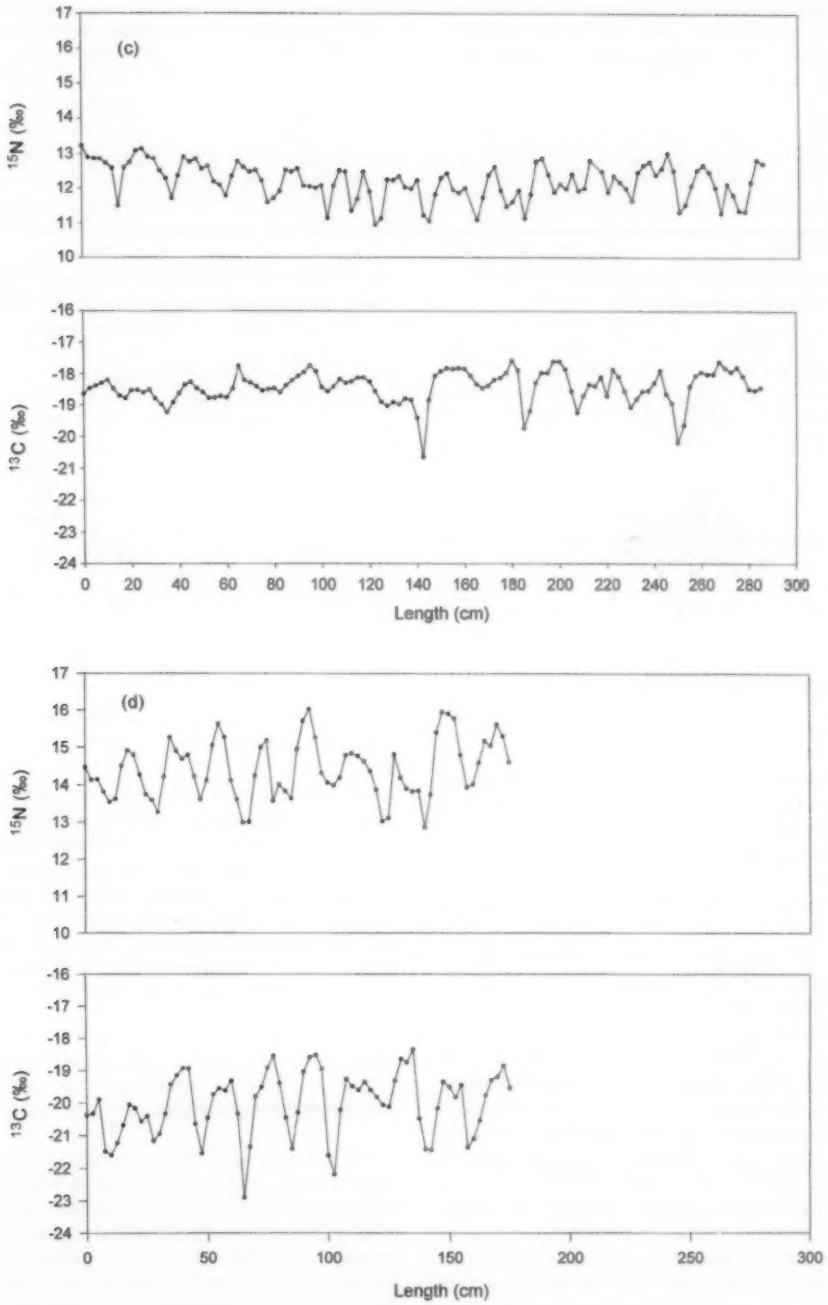
Fig. 1. Stable carbon and nitrogen isotope values along the length of baleen plates of eastern Arctic whale 96-02 (*a*), 96-03 (*b*), 88-01 (*c*), and western Arctic whale 96-01(*d*).



The third hypothesis that we considered for oscillating $\delta^{15}N$ but not $\delta^{13}C$ signatures in the baleen of eastern Arctic bowheads was that these animals underwent seasonal fasting during which catabolism of body muscle tissue occurred. This scenario was postulated by Best and Schell (1996) to account for observed enrichments in $\delta^{15}N$ in southern right whales (*Eubalaena australis*) during time spent in South African waters when carbon isotope ratios in baleen indicated that little or no feeding was occurring. Hobson et al. (1993) previously demonstrated that catabolism of muscle mass can

© 1998 NRC Canada

Fig. 1 (*concluded*).



lead to elevated $\delta^{15}N$ but not $\delta^{13}C$ signatures in captive and wild birds. If this occurs in bowhead whales, then we would expect elevated $\delta^{15}N$ signatures during fasting and lower values during periods of hyperphagia. Seasonal fasting occurs in other marine mammals including polar bears (*Ursus maritimus*; Atkinson and Ramsay 1995) and seals (Trites and Bigg 1996; Arnbom et al. 1997; Lydersen et al. 1997). However, loss of lean muscle mass may be rare compared with more labile fat reserves. Two of the eastern Arctic bowheads analyzed here (96-02, 96-03) were taken in late summer (August), and their $\delta^{15}N$ signatures of the basal (i.e., most recently grown) baleen tended to be declining prior to sharp

© 1998 NRC Canada

Table 2. Mean (± SD) stable nitrogen and carbon isotope values for all measurements along the length of baleen plates of eastern and western Arctic bowhead whales and for stable nitrogen isotope maxima and minima corresponding to oscillations depicted in Fig. 1.

Whale	Mean $\delta^{15}N$ (‰)	*n*	Range (‰)	Maximum $\delta^{15}N$ (‰)	*n*	Minimum $\delta^{15}N$ (‰)	*n*	Mean $\delta^{13}C$ (‰)	*n*	Range (‰)
Eastern Arctic										
96-02	12.9±0.4	113	12.0 to 13.7	13.3±0.2	20	12.4±0.2	19	−17.5±0.3	113	−18.5 to −16.8
96-03	14.5±0.4	37	13.7 to 15.2	14.9±0.2	6	14.2±0.3	6	−18.5±0.3	37	−19.1 to −18.0
88-01	12.2±0.5	113	11.0 to 13.2	12.6±0.3	20	11.5±0.3	20	−18.4±0.5	115	−20.7 to −17.6
Western Arctic										
96-01	14.4±0.8	71	12.9 to 16.0	15.3±0.5	10	13.4±0.3	9	−20.0±0.9	71	−22.9 to −18.4

Fig. 2. Pattern of stable carbon and nitrogen isotope ratios in baleen among eastern Arctic bowhead whales.

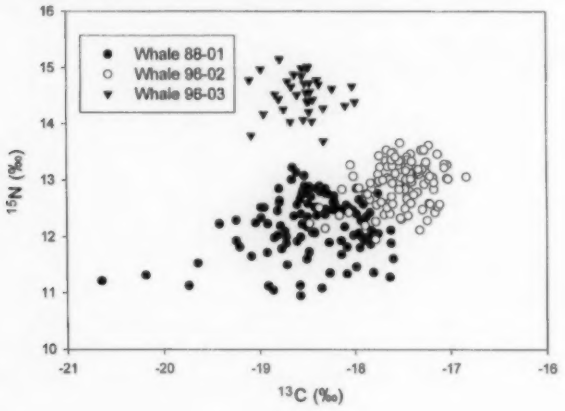
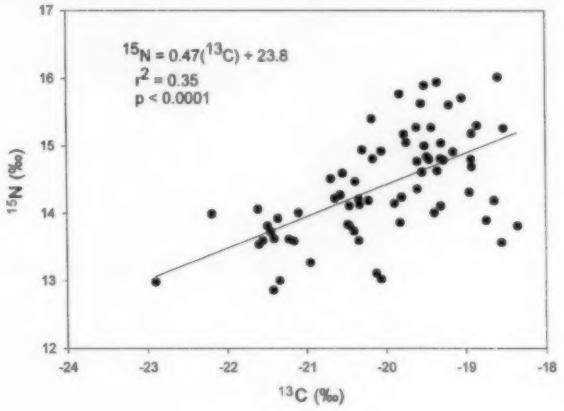


Fig. 3. Relationship between stable carbon and nitrogen isotope values in baleen of western Arctic whale 96-01.



increases that presumably corresponded to the previous few months (Schell and Saupe 1993). However, if fasting and the catabolism of protein reserves in these whales occurred during winter, following primary production peaks in the high Arctic (Welch et al. 1992), we would expect enriched $\delta^{15}N$ signatures in tissues to correspond to winter and not summer periods.

It is interesting to note that the young eastern Arctic whale (96-03) was generally enriched in $\delta^{15}N$ signatures in baleen compared with the other adult eastern Arctic animals. We suspect that this difference is due to the fact that young animals have isotopic signatures that reflect periods of nutrition prior to weaning when mother's milk, representing effectively a higher trophic-level food source, was consumed. This neonate enrichment effect has been observed previously in polar bears (Polischuk et al. 1999) and has been hypothesized for the $\delta^{15}N$ enrichment seen in the first tooth annuli of Steller sea lions (*Eumetopias jubata*; Hobson and Sease 1998).

Our isotopic investigation has provided evidence of nutritional or feeding changes that take place in eastern Arctic bowhead whales over their annual cycle. We have also demonstrated that the isotopic analysis of this population can provide a rapid and convenient technique for assessing minimum ages as well as differences in feeding location or nutritional history among individuals. Such information is almost impossible to obtain by more conventional approaches because these whales are simply inaccessible for most of the year and are not part of a regular legal hunt. Our results clearly demonstrate the importance of obtaining baleen samples from any eastern Arctic bowhead carcasses that become accessible. We also stress the need to more clearly delineate isotopic patterns in foodwebs in the eastern Arctic where whales occur. The continued isotopic sampling of whales and the foodwebs supporting them will undoubtedly provide new insights to the nutritional ecology of these marine mammals.

Acknowledgments

We thank K.J. Finley of Sidney, B.C., and Sue Cosens, Larry Dueck, and Harold (Buster) Welch of the Freshwater Institute (DFO) in Winnipeg for their advice and help in obtaining the baleen samples used in this study. Cory Gordon prepared samples for isotopic analysis at the Prairie and Northern Wildlife Research Center in Saskatoon. Garth Parry of the Department of Soil Science, University of Saskatchewan, Saskatoon, conducted stable-isotope analyses for K.A.H., and Norma Haubenstock, for D.M.S. This study was funded in part by the Canadian Wildlife Service, Prairie and Northern Region, and by the U.S. Minerals and Management Service, Anchorage, Alaska. Sue Cosens and Greg Rau provided valuable reviews that greatly improved this manuscript.

© 1998 NRC Canada

References

Altabet, M.A., and McCarthy, J.J. 1985. Temporal and spatial variations in the natural abundance of ^{15}N in PON from a warm-Core-Ring. Deep Sea Res. **37**: 755–772.

Arnbom, T., Fedak, M.A., and Boyd, I.L. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. Ecology, **78**:471–483.

Atkinson, S.N., and Ramsay, M.A. 1995. The effects of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). Funct. Ecol. **9**: 559–567.

Best, P.B., and Schell, D.M. 1996. Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. Mar. Biol. **124**: 483–494.

Bidigare, R.R., Fluegge, A., Freeman, K.H., Hanson, K.L., Hayes, J.M, Hollander, D., Jasper, J.P., King, L.L., Laws, E.A., Milder, J., Millero, F.J., Pancost, R., Popp, B.N., Steinberg, P.A., and Wakeham, S.G. 1997. Consistent fractionation of ^{13}C in nature and in the laboratory: growth-rate effects in some haptophyte algae. Global Biogeochem. Cycles, **11**: 267–278

Cosens, S.E., Qamukaq, T., Parker, B., Dueck, L.P., and Anardjuak, B. 1997. The distribution and numbers of bowhead whales, *Balaena mysticetus*, in northern Foxe Basin in 1994. Can. Field-Nat. **111**: 381–388.

Dunton, K.H., Saupe, S.M., Golikov, N., Schell, D.M., and Schonberg, S.V. 1989. Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. Mar. Ecol. Prog. Ser. **56**: 89–97.

France, R.L. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar. Ecol. Prog. Ser. **124**: 307–312.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. **33**: 1182–1190.

Hobson, K.A., and Sease, J.L. 1998. Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Steller sea lions. Mar. Mammal Sci. **14**: 116–129.

Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Progr. Ser. **84**: 9–18.

Hobson, K.A., Alisauskas, R.T., and Clark, R.G. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor, **95**: 388–394.

Hobson, K.A., Schell, D.M., Renouf, D., and Noseworthy, E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can. J. Fish. Aquat. Sci. **53**: 528–533.

Laws, E.A., Popp, B.N., Bidigare, R.R., Kennicutt, M.C., and Macko, S.A. 1995. Dependence of phytoplankton carbon isotopic composition on growth rates and $[CO_2]_{aq}$: theoretical considerations and experimental results. Geochim. Cosmochim. Acta, **59**: 1131–1138.

Lowry, L.F. 1993. Foods and feeding ecology. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Soc. Marine Mammal. Spec. Publ. No. 2. Allen Press, Lawrence, Kan. pp. 201–238.

Lydersen, C., Kovacs, K.M., and Hammill, M.O. 1997. Energetics during nursing and early postweaning fasting in hooded seal (*Cystophora cristata*) pups from the Gulf of St. Lawrence, Canada. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. **167**: 81–88.

Michener, R.H., and Schell, D.M. 1994. Stable isotope ratios as tracers in marine and aquatic food webs. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific Publications, Oxford. pp. 138–157.

Moore, S.E., and Reeves, R.R. 1993. Distribution and movement. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Soc. Mar. Mammal. Spec. Publ. No. 2. Allen Press, Lawrence, Kan. pp. 313–386.

Parker, P.L. 1962. The isotopic composition of the carbon of fatty acids. Annual Report 1961–1962. Carnegie Institute, Washington, D.C.

Polischuk, S.C., Hobson, K.A., and Ramsay, M.A. 1999. Use of stable-carbon and nitrogen isotope analysis to investigate fasting and time of weaning in female polar bears and cubs. Mar. Mam. Sci. In press.

Rau, G.H., Riebesell, U., and Wolf-Gladrow, D. 1996. A model of photosynthetic ^{13}C fractionation by marine phytoplankton based on diffusive molecular CO_2 uptake. Mar. Ecol. Prog. Ser. **133**: 275–285.

Schell, D.M., and Saupe, S.M. 1993. Feeding and growth as indicated by stable isotopes. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Soc. Mar. Mammal. Spec. Publ. No. 2. Allen Press, Lawrence, Kan. pp. 491–509.

Schell, D.M., Saupe, S.M, and Haubenstock, N. 1989*a*. Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}C$ techniques. Mar. Biol. **103**: 433–443.

Schell, D.M., Saupe, S.M., and Haubenstock, N. 1989*b*. Natural isotope abundances in bowhead whale (*Balaena mysticetus*) baleen: markers of aging and habitat usage. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer Verlag, New York. pp. 261–269.

Schell, D.M., Barnett, B.A., and Vinette, K. 1998. Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort Seas. Mar. Ecol. Prog. Ser. **162**: 11–23

Trites, A.W., and Bigg, M.A. 1996. Physical growth of northern fur seals (*Callorhinus ursinus*): Seasonal fluctuations and migratory influences. J. Zool. (London), **238**: 459–482.

Welch, H.E., Bergmann, M.A., Sifferd, T.D., Martin, K.A., Curtis, R.E., Crawford, R.E., Conover, R.J., and Hop, H. 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. Arctic, **45**: 343–357.

Wong, W., and Sackett, W.M. 1978. Fractionation of stable carbon isotopes by marine phytoplankton. Geochim. Cosmochim Acta, **42**: 1809–1815.

Zeh, J.E., Clark, C.W., George, J.C., Withrow, D., Carroll, G.M., and Koski, W.R. 1993. Current population size and dynamics. *In* The bowhead whale. *Edited by* J.J. Burns, J.J. Montague, and C.J. Cowles. Soc. Mar. Mammal. Spec. Publ. No. 2. Allen Press, Lawrence, Kan. pp. 409–490.

© 1998 NRC Canada

Spatiotemporal modelling for the annual egg production method of stock assessment using generalized additive models

N.H. Augustin, D.L. Borchers, E.D. Clarke, S.T. Buckland, and M. Walsh

Abstract: Generalized additive models (GAMs) are used to model the spatiotemporal distribution of egg density as a function of locational and environmental variables. The main aim of using GAMs is to improve precision of egg abundance estimates needed for the annual egg production method. The application of GAMs requires a survey design with good coverage in space and time. If the only results available are from less optimal survey designs, they can be improved by using historical data for spawning boundaries. The method is applied to plankton egg survey data of Atlantic mackerel (*Scomber scombrus*) in 1995. The GAM-based method improves the precision of estimates substantially and is also useful in explaining complex space–time trends using environmental variables.

Résumé : Des modèles additifs généralisés sont utilisés pour modéliser la distribution spatio-temporelle de la densité des oeufs en fonction de variables géographiques et environnementales. Le but principal des modèles additifs généralisés est d'améliorer la précision des estimations de l'abondance des oeufs nécessaires dans la méthode de détermination de la production annuelle d'oeufs. L'application de ces modèles exige un protocole d'échantillonnage offrant une bonne couverture dans le temps et dans l'espace. Si on dispose seulement de résultats provenant de relevés moins valables, on peut améliorer ces résultats en utilisant des données historiques relatives aux frontières des aires de fraye. On applique ici la méthode aux données issues d'un relevé des oeufs planctoniques du maquereau (*Scomber scombrus*) effectué en 1995. La méthode fondée sur les modèles additifs généralisés accroît substantiellement la précision des estimations et est aussi utile pour expliquer des tendances spatio-temporelles complexes au moyen de variables environnementales.

[Traduit par la Rédaction]

Introduction

Generalized additive models (GAMs) provide a powerful and flexible statistical tool for modelling spatiotemporal distributions of animal abundance from survey data. They have previously been applied to relate fish survey or abundance data to locational and environmental covariates, e.g., in Swartzman et al. (1992, 1994, 1995), Welch et al. (1995), Maravelias and Reid (1997), and Swartzman (1997). Wood and Horwood (1995) related sole egg abundance data to locational variables only using thin-plate splines. All of these applications have the emphasis on applying GAMs to explore relationships between abundance and environmental and (or) locational variables; they do not attempt to produce reliable abundance estimates. Swartzman et al. (1992) gave abundance estimates for Bering sea groundfish survey data, but found substantial downward bias in their estimates compared with estimates using design-based methods. Deriso et al. (1996) estimated an abundance index for Pacific sardine using GAMs, but only used relative abundance estimates. Borchers et al. (1997*b*) went one step further and used GAMs to model egg density as a function of locational and environmental variables to obtain egg abundance estimates for the daily egg production method (DEPM). Here, we want to improve upon the traditional annual egg production method (AEPM) by modelling egg density survey data as a smooth function of space, time, and oceanographic variables and thus improve precision of egg abundance estimates. The AEPM and DEPM estimate total fish biomass indirectly from an estimate of the total annual egg production and daily egg production, respectively (for details, see Gunderson 1993; Anonymous 1994). In contrast with commercial catch-based methods, they provide (like acoustic surveys) a fishery independent estimate of stock size. The AEPM requires egg plankton surveys of the spawning area at multiple time points through the spawning season, so that egg production can be estimated at each time point of the spawning season. In the DEPM, egg production is only estimated at a single point in time. While a single survey with sufficient spatial coverage, ideally at a single point in time, is adequate for the application of GAMs to the DEPM, successful spatiotemporal modelling of egg abundance for the AEPM requires adequate coverage of the survey area in both

Received February 9, 1998. Accepted September 11, 1998.
J14423

N.H. Augustin.[1] Biomathematics & Statistics Scotland (BioSS), Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, U.K.
D.L. Borchers, E.D. Clarke, and S.T. Buckland. Research Unit for Wildlife Population Assessment, University of St Andrews, St Andrews, Fife KY16 9SS, U.K.
M. Walsh. Scottish Office Agriculture and Fisheries Department, Marine Laboratory Aberdeen, P.O. Box 101, Victoria Road, Aberdeen, U.K.

[1]Author to whom all correspondence should be addressed.
e-mail: nicole@bioss.sari.ac.uk

© 1998 NRC Canada

space and time. Logistically, it is impossible to cover the whole survey area instantaneously at any given time, and effects of space and time will always be confounded to some degree. We present GAM-based methods for spatiotemporal modelling that are robust to the effects of this sort of confounding. We illustrate the methods using the 1995 egg survey data of the western stock of Atlantic mackerel (*Scomber scombrus*).

When modelling egg production, the random variable observed is egg count. Although we are interested in egg production, egg count as a response variable in the model is a natural choice, and there are several distributions that can be used for such a response variable. The conversion of counts into egg production estimates can be handled by specifying an offset comprising the conversion factors required. Swartzman et al. (1992) used counts in their GAM as the response variable, but obtained estimates 30–50% lower than estimates from design-based methods. Borchers et al. (1997*b*) used counts as response in their GAM for the DEPM, and their abundance estimate for Atlantic mackerel was 20% lower than the estimate obtained from the traditional method. We illustrate how such a count model in the presence of subsampling can lead to biased estimates from the GAM-based methods and how this bias can be avoided. Finally, we compare the performance of the GAM-based AEPM with that of the traditional AEPM.

Methods

Traditional AEPM

In the traditional AEPM, egg surveys are carried out during a number of periods through the spawning season, and estimates for each period are assigned to the midpoint of the period. The egg production curve is estimated by plotting these estimates against time and joining the estimates, either by straight lines or by using a nonlinear function such as cubic smoothing splines (Gunderson 1993). Total annual egg production (E_a) is estimated by integrating under the curve.

The area of spawning is usually divided into strata and random samples are taken in each stratum and in each survey period. The multiple egg surveys carried out throughout the spawning period are designed to provide full spatial coverage of the spawning area in each survey period. Mean daily egg production is estimated for each stratum and survey period, for example, by estimating egg production per grid square and summing these estimates over the grid squares in the stratum. The estimated total daily egg production by period is then obtained by summing over strata.

Variance estimation is based on the assumption that observed egg numbers are distributed with a constant coefficient of variation (CV) in space and time (Anonymous 1996). When the egg production curve is assumed to be piecewise linear, as is the case with the AEPM as applied to Atlantic mackerel, the estimated variance for total annual egg production neglects the component of variance due to estimating the shape of the egg production curve.

GAM-based AEPM

Although the traditional method treats data from each survey period as if they came from a single point in time (the survey period midpoint), sampling within each period is spread over time. Here, we treat time as continuous and model egg density as a function of location, oceanographic variables, and time using GAMs. GAMs are an extension of generalized linear models (GLMs) (McCullagh and Nelder 1989). Both accommodate a variety of distributions for the response, but unlike GLMs, GAMs allow flexible nonlinear effects of the covariates on the response to be estimated from the data. GAMs have the following general form (Hastie and Tibshirani 1990):

$$E[y] = g^{-1}\left(\beta_0 + \sum_k S_k(x_k)\right)$$

The function $g(\cdot)$ is the link function, which defines the relationship between the response and the linear predictor, $\beta_0 + \sum_k S_k(x_k)$. The response, y, is assumed to be distributed according to one of a wide family of statistical distributions. The term x_k is the value of the kth spatial covariate, such as location or date, β_0 is an intercept term, and $S_k(\cdot)$ is a one-dimensional smoothing function for the kth covariate. The degree of smoothing performed by a smoother $S_k(\cdot)$ is determined by the number of neighbouring points used for the smoothed estimates. We use cubic spline smoothers for $S_k(\cdot)$, where the degrees of freedom (df) associated with the smoother control the amount of smoothing; the fewer the degrees of freedom, the greater the smoothing. For example, df = 1 corresponds to a linear effect of the associated covariate, as in a GLM. For count data, a common choice is a Poisson distribution with a log link function. The choice of distribution is intrinsically linked with the assumed relationship between y and its variance. For example, the Poisson distribution assumes that the variance is equal to the mean ($\mathrm{Var}(y) = \mu$, where μ is the expectation of the response), an overdispersed Poisson distribution assumes that the variance is a multiple of the mean ($\mathrm{Var}(y) = \sigma^2\mu$, where σ^2 is the dispersion parameter), and the negative binomial distribution assumes $\mathrm{Var}(y) = \mu + \mu^2/k$. The negative binomial distribution allows for more variation in the response than the Poisson distribution through the term μ^2/k. The parameter k is fixed, i.e., it can be set by the user, and is also called the aggregation parameter. The greater k, the more similar the negative binomial distribution is to the Poisson distribution.

GAMs for egg density

Three possible types of response are egg density, egg counts, and egg presence/absence in a sample. Use of the latter is not illustrated here but is useful in cases where zero eggs are observed over a large part of the survey area; then, egg density can be modelled in two stages, with one model for the presence/absence of eggs (stage 1) and a second model for nonzero egg counts (stage 2). This procedure is described in Borchers et al. (1997*b*).

When it comes to choosing the response in the GAM for modelling egg density, it is useful to envisage the sampling process. The eggs obtained from a plankton sample are easily counted, but staging the eggs is more time consuming. Therefore, subsamples for egg staging are typically taken in high-density areas whereas in low-density areas, all sampled eggs might be staged. For different plankton samples, there will be a similar number of eggs in the subsample, but the egg density in the sampled areas will vary considerably. If several vessels are involved in the survey, there might be other differences in the sampling process, e.g., longer hauls will result in higher egg counts, as will the use of sampling nets with a larger opening.

The number of eggs counted (n_{ij}) at a given stage is converted into egg density ($\mathrm{density}_{ij}$) per day per square metre by multiplying by the following conversion factor (conv_{ij}):

$$\mathrm{conv}_{ij} = \frac{\mathrm{ns}_{ij}}{\mathrm{nsub}_{ij}} \cdot \frac{\mathrm{depth}_{ij}}{\mathrm{volume}_{ij}} \cdot \frac{1}{\mathrm{duration}_{ij}} \cdot \mathrm{mort.\ adj.}$$

where i is the index for location, j is the index for sampling day, "ns" represents the number of eggs of all stages in the sample, "nsub" represents the number of eggs of all stages in the subsample, "depth" is the depth of the water column sampled, "vol-

© 1998 NRC Canada

ume" is the water volume sampled, "duration" is the duration of the selected stage, and "mort.adj." is an egg mortality adjustment (see Gunderson 1993 for further details).

Density model

If we choose density as the response variable, the best choice of distribution for the response is not obvious. A normal distribution with an identity link can lead to negative estimates of density in some localities at some occasions, and while the actual distribution of egg density is often appreciably skewed, the normal is symmetric. A Poisson, gamma, or negative binomial distribution might therefore be more appropriate.

Our model for expected egg density, $E[\text{density}_{ij}]$, of a given stage in the sample from location i and at day j with j = minday,..., maxday ("minday" and "maxday" are the first and last days with data available) is as follows:

$$(1)\qquad E[\text{density}_{ij}] = \exp\left(\beta_0 + \sum_k S_k(x_{kij}) + \sum_{k=1}^{K}\sum_{l>k}^{K} S_{kl}(x_{kij} \times x_{lij})\right)$$

where a log link function is used and $\exp(\cdot)$ is the inverse of the log link function, x_{kij} represents the kth covariate at the ith location on day j, β_0 is the intercept parameter, $S_k(\cdot)$ is the smoothing spline for the kth covariate, and $S_{kl}(\cdot)$ is the smoothing spline for the interaction term of the kth and lth covariates. Given estimates $\hat{\beta}_0$, $\hat{S}_k(\cdot)$, and $\hat{S}_{kl}(\cdot)$ (k = 1,..., K; l = 1,..., K), the expected egg density at a point with covariates x_k (k = 1,..., K) is given by

$$\hat{E}[\text{density}_{ij}] = \exp\left(\hat{\beta}_0 + \sum_{k=1}^{K} \hat{S}_k(x_{kij}) + \sum_{k=1}^{K}\sum_{l>k}^{K} \hat{S}_{kl}(x_{kij} \times x_{lij})\right)$$

Count model

In the absence of subsampling, the preferred choice is to model the number of eggs observed in the sample n_{ij} from location i at day j (y_{ij}; j = minday,..., maxday) using a GAM with an appropriate distribution (e.g., Poisson, gamma, or negative binomial) and link function. However, in areas of high egg density, the sample of eggs is typically subsampled to save time. Thus the volume of water sampled corresponding to a given count tends to be small when egg density is high. The assumed mean–variance relationship for counts does not reflect the mean–variance relationship of egg density. GAMs use the variance of the response (counts in this case) to construct weights in the iterative fitting procedure. When the error distribution is Poisson, the weights are equal to the mean response. This response is systematically reduced in areas of high density by the subsampling procedure, so that too little weight is attached to data from such areas, and this leads to bias.

The count model with a log link may be expressed as

$$(2)\qquad E[n_{ij}] = \exp\left(\text{offset}_{ij} + \beta_0 + \sum_k S_k(x_{kij}) + \sum_{k=1}^{K}\sum_{l>k}^{K} S_{kl}(x_{kij} \times x_{lij})\right)$$

where $\text{offset}_{ij} = -\log(\text{conv}_{ij})$. Given estimates $\hat{\beta}_0$, $\hat{S}_k(\cdot)$, and $\hat{S}_{kl}(\cdot)$ (k = 1,..., K; l = 1,..., K), the expected egg density at a point with covariates x_k (k = 1,..., K) is given by setting the "offset" term to zero:

$$\hat{E}[\text{density}_{ij}] = \exp\left(\hat{\beta}_0 + \sum_{k=1}^{K} \hat{S}_k(x_{kij}) + \sum_{k=1}^{K}\sum_{l>k}^{K} \hat{S}_k(x_{kij} \times x_{lij})\right)$$

Integration over space and time

Once a model has been selected, the GAM provides a smooth expected egg density surface that is integrated numerically over space, within the survey area, and time, within the spawning period, to provide an estimate of the total egg production in the survey area (Fig. 1). Moreover, by integrating over the appropriate spatial and temporal limits, egg production can be estimated at any spatial and (or) temporal resolution. In particular, the method can provide estimates of daily egg production at any given day in the spawning period over the whole spawning area, as well as an estimate of annual egg production (E_a).

In order to integrate the estimated egg production surface over space and time, the surface must be evaluated at points other than those at which samples were obtained. Explanatory variables that are not well defined except at sampled points and times (e.g., duration of haul and sampling depth) present difficulties in this regard and should be excluded as candidate covariates. Time-dependent covariates are also only available at the sampled points and times. In order to use these covariates in integrating the egg production surface to obtain the egg production curve, they would have to be modelled as functions of space and time. This would add another dimension to the modelling problem, which we do not address.

Dealing with sparse survey coverage

Unless the spawning area is small relative to sampling resources available, surveys will rarely cover the complete spawning area. If observed egg densities at the outer limits of the sampled area are greater than zero, spatial and temporal extrapolation into unsampled regions of the spawning area can lead to positive bias. This can be avoided by defining outer boundaries beyond which spawning is known not to occur and constraining the fitted models to be zero (or nearly zero) at those points. Often, historical data help to define these outer boundaries of spawning. In most cases, these spatial boundaries will vary over time. Inadequate coverage in the time dimension can be dealt with similarly. The fitted models can be constrained at the beginning and the end of spawning by specifying times before which spawning would not have begun and after which spawning will have ended. Artificial data points with zero egg density along the spatial boundaries, and scattered over the whole survey area at the temporal limits, are added to the data. The additional data points are referred to as "structural zeros" and are used in estimation, model selection, and variance estimation.

Model selection

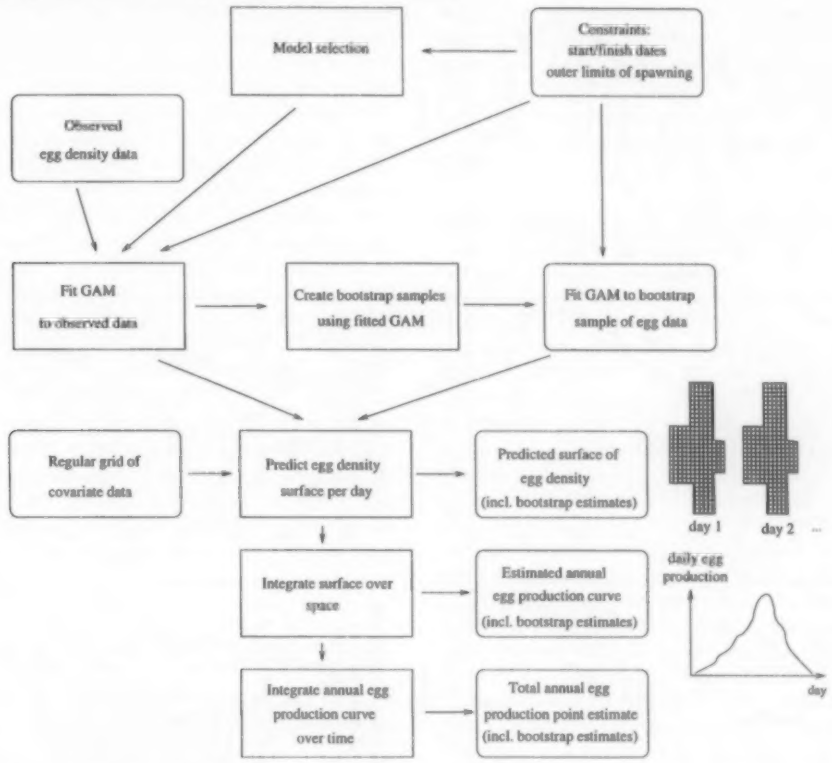
Model selection with GAMs involves choosing a distribution for the response, a link function, an appropriate set of covariates, and appropriate degrees of freedom for smoothing the covariates. We used plots of deviance residuals standardized by their estimated variance versus fitted values to examine the appropriate link function and distribution used. To examine whether the spatial distribution was adequately modelled, we plotted averages of deviance residuals by grid square and month.

Variance estimation

The variance of the annual egg production estimator $\hat{E}_a$ can be estimated using parametric bootstrap procedures. This involves generating b pseudo-samples of the egg survey data using the fitted model and refitting the GAM to each of these pseudo-samples. For instance, for a model using the negative binomial (NB) distribution, a pseudo-sample at location i and at day j is produced by

© 1998 NRC Canada

Fig. 1. Schematic representation of the GAM egg production method. Boxes with rounded corners correspond to input data and output estimates; boxes with square corners correspond to estimation procedures.



sampling from $NB(\hat{\mu}_{ij}, k)$, where k is fixed and $\hat{\mu}_{ij}$ is the fitted value. Integrating each refit over space and time yields b bootstrap estimates for E_n. The CV of these bootstrap estimates is the estimate of the CV for the GAM estimate. Bootstrap percentile confidence intervals (Efron and Tibshirani 1993) can also be constructed from the b bootstrap estimates. The bootstrap procedure can generate variance estimates for egg production estimates at any spatial and (or) temporal resolution. Figure 1 gives an overview of the estimation procedure for the GAM-based AEPM.

Example: western Atlantic mackerel 1995 egg survey data

The International Council for the Exploration of the Sea (ICES) has carried out triennial Atlantic mackerel and horse mackerel (*Trachurus trachurus*) egg surveys since 1977. We illustrate the GAM method using the 1995 ICES survey data of the "western" Atlantic mackerel stock. This survey was conducted by England, Germany, Ireland, The Netherlands, Norway, Portugal, Scotland, and Spain. Plankton sampling was carried out by national versions of a Gulf III type sampler with the exception of Spain, which used bongo and Pairovet samplers (Anonymous 1996). Although the stock assessments for the series of ICES surveys currently use the traditional AEPM, the GAM-based AEPM has been applied to data from three surveys (1989, 1992, and 1995) of the western area and from the 1995 survey of the southern area (Borchers et al. 1997*a*).

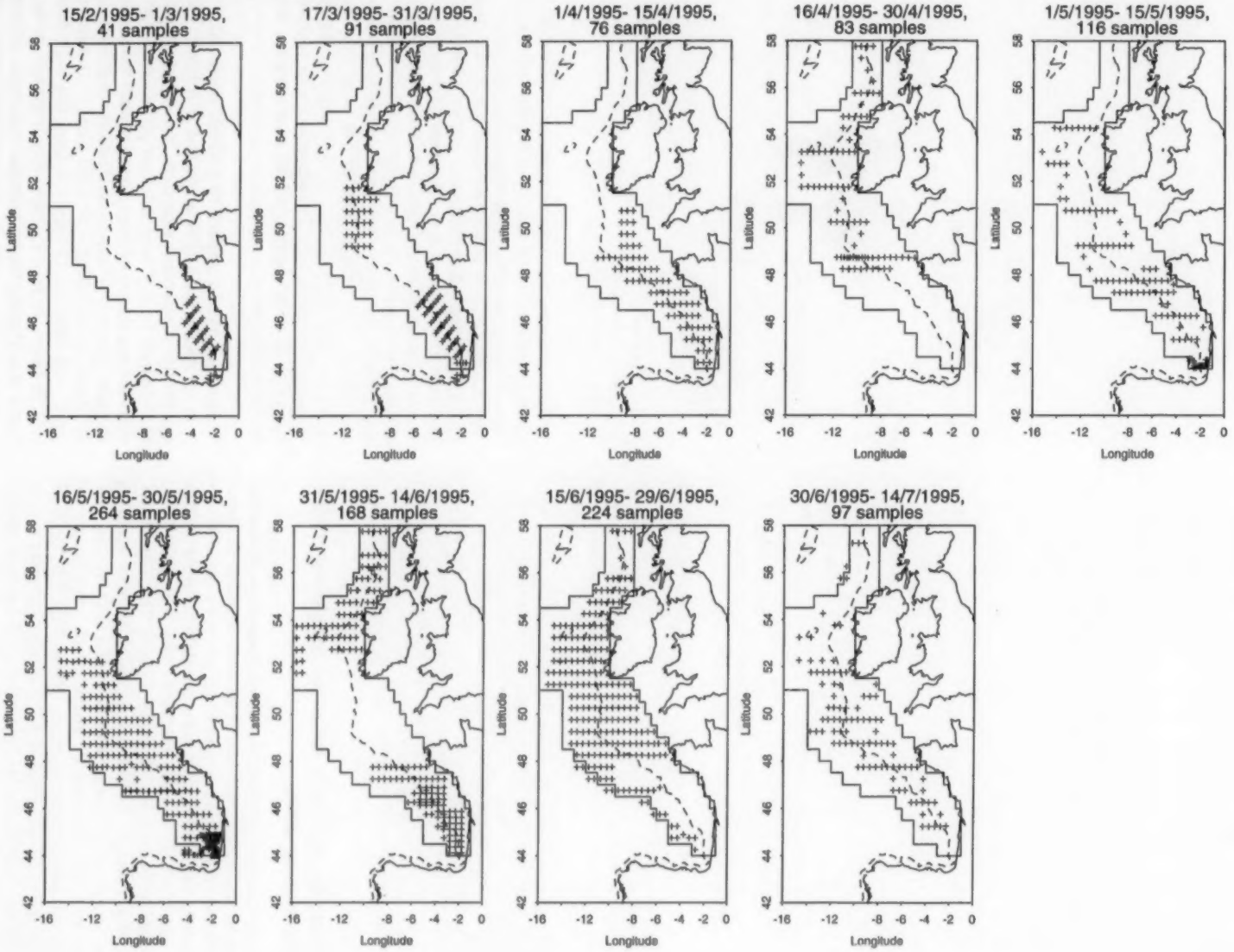
Figure 2 shows the Atlantic mackerel 1995 survey coverage over intervals of 15 days spanning the sampling period. Note that there is only partial spatial coverage of the survey area during any time period. For example, in the beginning of the survey period in February, samples are only taken in the south of the survey area. This confounding of sampling in space and time makes it difficult to distinguish the effects of time and space at the beginning of the survey. An adaptive sampling strategy in the east–west direction was used in this survey. This strategy ensured that outer boundaries of spawning were sampled even if these extended beyond the "standard" sampling area. In comparison with previous survey years, the 1995 survey had the most complete coverage in space and time.

Traditional AEPM applied to Atlantic mackerel

In the traditional AEPM as applied to Atlantic mackerel, egg density is estimated separately in each survey rectangle (0.5° latitude by 0.5° longitude) per period, using the mean observed egg density of stage 1 eggs in each rectangle as the estimate. The survey was divided into seven periods: (*i*) 16–25 March, (*ii*) 26 March – 14 April, (*iii*) 15–21 April, (*iv*) 22 April – 16 May, (*v*) 17 May – 8 June, (*vi*) 9–29 June, and (*vii*) 30 June – 16 July. Egg mortality is ignored on the basis that it is negligible for the youngest egg stage, although ignoring mortality results in slight underestimation of biomass. For unsampled rectangles that are adjacent to at least two sampled rectangles and within the survey area, egg den-

© 1998 NRC Canada

Fig. 2. Locations of egg samples taken during the 1995 Atlantic mackerel survey. Samples are shown summarized in 15-day intervals. The broken line represents the 200-m contour line; the solid line represents the survey area.



© 1998 NRC Canada

sity is estimated by the arithmetic mean of the densities in adjacent rectangles. Other unsampled rectangles within the survey area are assumed to have zero egg density. Estimates of egg density within each rectangle are converted to estimates of egg abundance by multiplying them by the surface area of the associated survey rectangle. Total egg production in a single period is estimated by the sum of the estimates of egg abundance in each rectangle, over all rectangles in the survey region. The estimated egg abundance from each period is assigned to the period midpoint, and egg abundance between these period midpoints is estimated by linear interpolation. In order to estimate the total egg production over the whole survey period, an initial and a final time point, at which there are assumed to be no eggs in the area, are chosen. These two time points define the limits of the spawning period. Annual egg production is estimated by integrating under this piecewise linear egg production curve over the whole spawning period (Anonymous 1996).

Data for estimating the initial time point (the last time before the survey at which there were no eggs) and the final time point (the first time after the survey at which there were no eggs) are scant, as there are no directed surveys in these periods. Although all available data are used to decide where to locate the points in time, their date is necessarily somewhat arbitrary.

Start and finish dates and outer limits of spawning for the GAM-based AEPM

In 1995, sampling for Atlantic mackerel seldom spanned the entire spawning area, and sampling did not span the entire temporal range of spawning. This is apparent from observed egg densities (Fig. 3) at the outer limits of the sampled area and at the latest sample times. In both cases, egg densities were often substantially greater than zero. In order to avoid positive bias being introduced by spatial and temporal extrapolation into unsampled regions of the spawning area at any time, the outer boundaries of spawning were defined prior to fitting the GAMs, and the fitted models were constrained to be close to zero at these outer boundaries by using structural zeros, as described above. The spatial boundaries that we used vary over time, in accordance with what are believed to be conservative estimates of the true outer boundary of spawning at various times through the spawning season (i.e., the true boundaries are likely to be within the assumed boundaries). The locations of these boundaries are based on data from all surveys of the area conducted up to 1995. Each of the five months between March and July was assigned a different spatial boundary defined by appropriately placed structural zeros (Fig. 4). Except in July, no outer boundary was specified at the southern end of the western survey area. Egg densities there were high, and counts were made south of the boundary for stock assessment in the southern area. We included these counts to improve the fit of the GAM at the boundary. Spatial boundaries were chosen as follows. Using a grid of 0.5° latitude by 0.5° longitude, and extracting by grid rectangle the maximum egg density observed between 1977 and 1995, the boundary was defined to be the first rectangle that lay at least 0.5° longitude beyond the outermost rectangle with zero or near-zero egg density. These rules were not always rigidly adhered to but were adjusted slightly in the light of additional data from other sources.

A temporal limit at which it was assumed that spawning had not yet begun and a temporal limit at which it was assumed that spawning had ended were defined and used similarly. The start date (minday) for spawning was assumed to be 10 February and the finish date (maxday) was assumed to be 31 July. The same dates were used for the traditional AEPM.

Model selection for the GAM-based AEPM

To simplify the model selection process, we adopted the approach taken by Borchers et al. (1997*b*) for model selection and considered only spline smoothers with either df = 4 or df = 1 for covariates and their first-order interactions. The covariates first entered the model with df = 4, and backward stepwise elimination was used to select a set of covariates. Selection between smoothers with df = 4 and smoothers with df = 1 was performed in the next step. Finally, first-order interactions of the previously selected covariates were first entered with df = 4, again using backwards stepwise elimination for model selection, and selection between smoothers with df = 4 and df = 1 was performed in the next step. Comparisons between models were made on the basis of approximate F tests (Hastie and Tibshirani 1990). The covariates (x_k) used in the GAMs are as follows: date, date (days) since 1 January; lat, latitude (degrees); lon, longitude (degrees); cdist, closest distance (nautical miles) to the 200-m depth contour line (negative if bottom depth > 200 m; the 200-m contour line corresponds to the edge of the continental shelf); gdist, distance (nautical miles) along the 200-m contour line in a north–south direction; and log(depth), logarithm of bottom depth (metres).

Substantial confounding between position, time, and vessel precluded inclusion of a vessel factor. Sea surface temperature at a given location was found to be highly correlated with date. We chose to include date in preference to sea surface temperature, as this avoids difficulties associated with predicting temperature at unsampled points. Aside from date, all covariates used in the model are constant with respect to time and all are known over the full range of the survey. The digitized bathometry data set (DBDB5) of the British Oceanographic Data Centre has been used to obtain bottom depths.

While models were selected using structural zeros to constrain the fitted model to be at zero or close to zero at the spatial and temporal boundaries of spawning, the contribution from these structural zeros to the deviance was removed before comparing models.

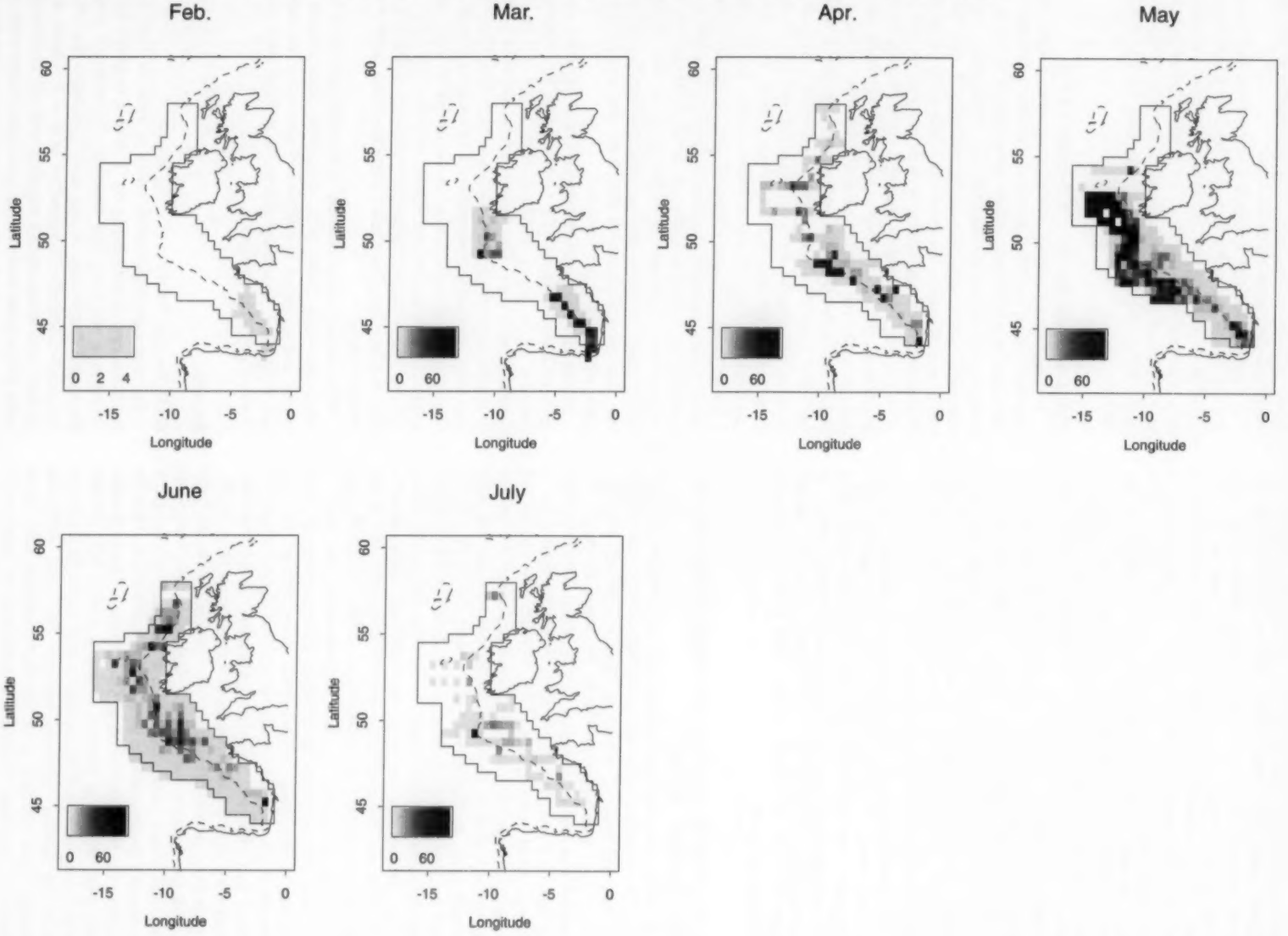
Results

GAM for egg density

Because subsamples were taken in areas of high density, we fitted egg density using eq. 1 with a negative binomial distribution and a log link function. The selected model for the spatial distribution of egg density includes the following covariates selected with smoothers of df = 4: s(date), s(cdist), s(gdist), and s(log(depth)) together with all smoothed first-order interactions between the covariates except cdist × gdist and cdist × log(depth). The residual deviance for this model

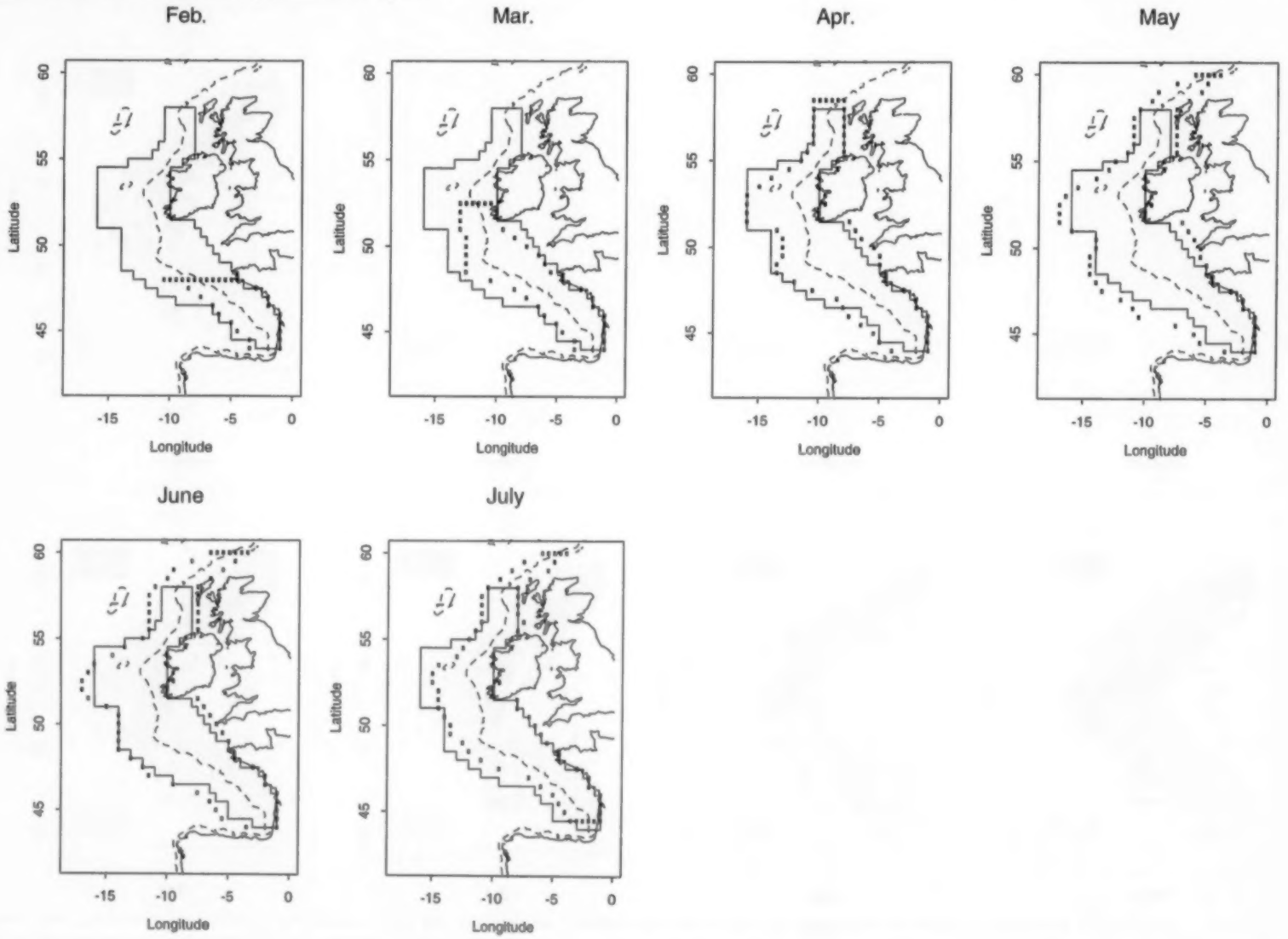
© 1998 NRC Canada

Fig. 3. Observed mackerel egg densities (eggs·m^{-2}·day^{-1}) averaged within each half-degree block in the survey area. Unshaded half-degree blocks were not sampled. The broken line represents the 200-m contour line; the solid line represents the survey area. The same scale of shading is used for all plots.



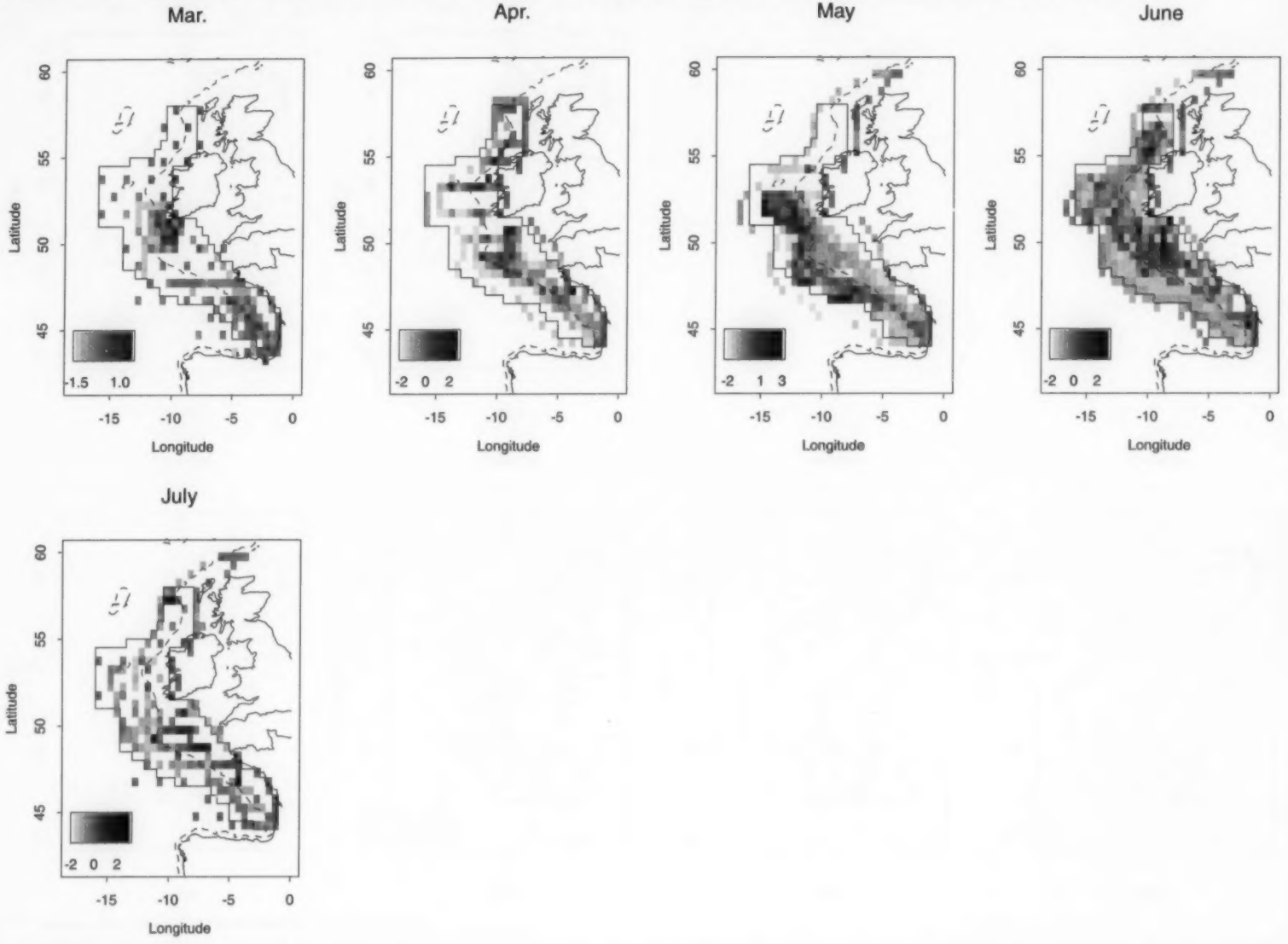
© 1998 NRC Canada

Fig. 4. Assumed outer limits of spawning for Atlantic mackerel in the survey area. The solid squares indicate the locations of structural zeros. The broken line represents the 200-m contour line; the solid line represents the survey area.



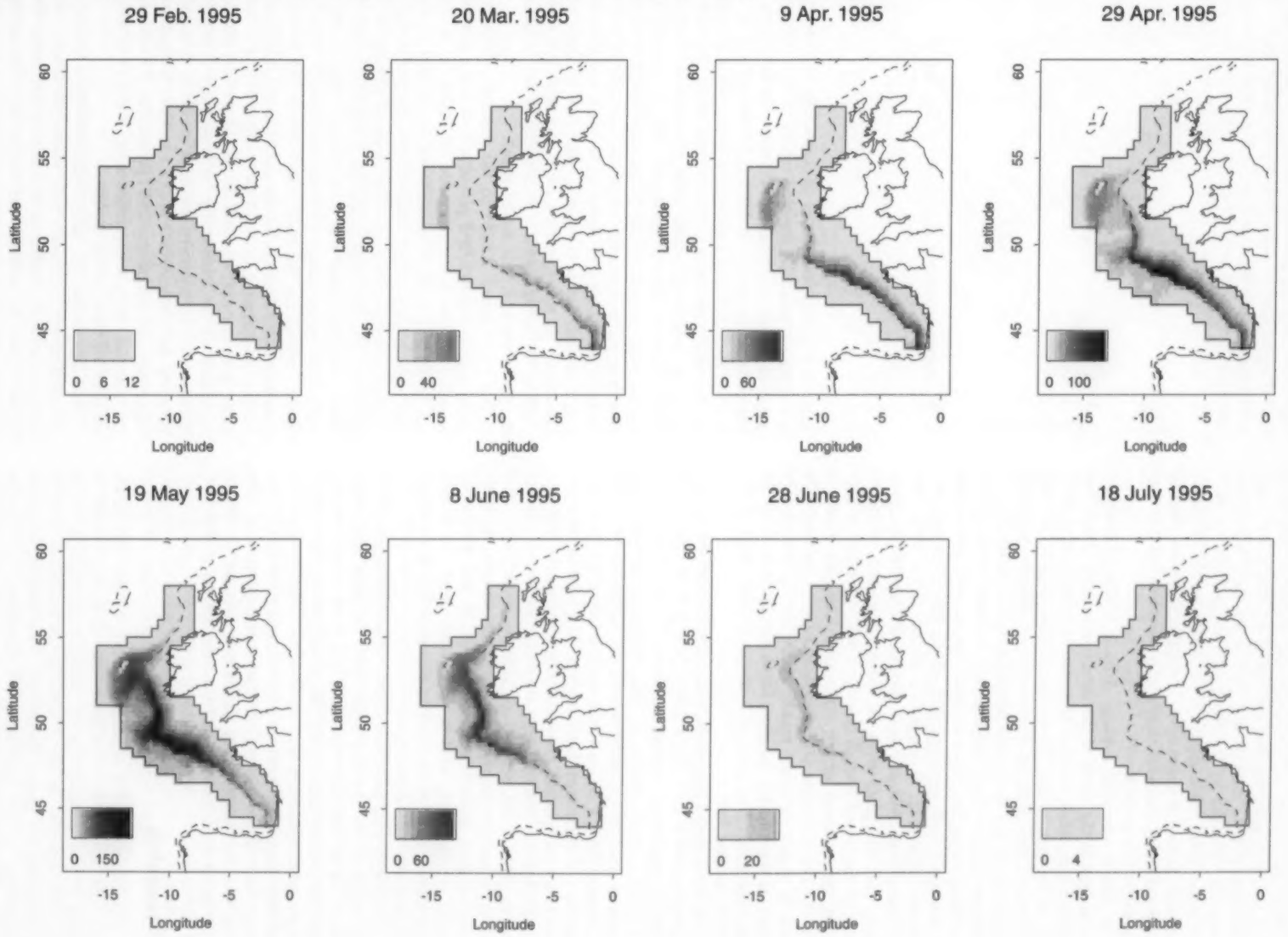
© 1998 NRC Canada

Fig. 5. Spatial distribution of standardized deviance residuals summarized by month for the density model (response is density) with df = 4 fitted to the 1995 Atlantic mackerel survey data. The broken line represents the 200-m contour line; the solid line represents the survey area. The same scale of shading is used for all plots.



© 1998 NRC Canada

Fig. 6. Spatial distribution of estimated Atlantic mackerel egg density (eggs·m^{-2}·day^{-1}) in 1995 using the density model at selected dates in 20-day intervals. The broken line represents the 200-m contour line; the solid line represents the survey area. The same scale of shading is used for all plots.



© 1996 NRC Canada

is 1826 on 1587 df, with an estimated dispersion parameter of 1.1, which indicates that the model fits fairly well. Approximate F tests indicate that date is the most significant covariate, followed by log(depth). Deviance residuals plotted versus fitted value appear to be fairly random. Deviance residuals plotted in space (Fig. 5) suggest that there may be some remaining unmodelled spatial correlation, but it is negligible for our purpose.

In March, observed average Atlantic mackerel densities are highest in the south of the survey area along the 200-m contour line, while in May, high densities are further north and to the west of the 200-m contour line (Fig. 3). A comparison of the observed distribution of Atlantic mackerel eggs (Fig. 3) and the predicted spatial egg densities (Fig. 6) indicates that the model has captured the south–north shift in spawning along the 200-m contour line, as well as the peak in abundance and westward shift during May. The egg production curve (Fig. 7) suggests a slightly lower peak than the curve from the traditional method, but overall, it agrees fairly well. The plots using the centred covariates of the effects of the partial smooth functions, e.g., the effect of date given the inclusion of the other covariates, are given in Fig. 8. The smoother corresponding to date indicates the peak of spawning in the middle of the survey period. The effect of the smooth function fitted for distance from the 200-m contour line (Fig. 8*a*) shows a peak west of the 200-m contour line.

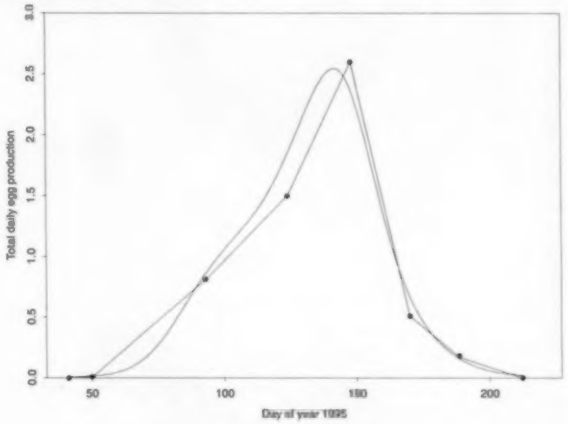
The total annual egg production estimate from the density model is 1.49×10^{15} (SE = 0.10, CV = 6.9) in comparison with the traditional method estimate of 1.48×10^{15} (SE = 0.17, CV = 11.5) (Table 1). The difference between estimates is small in comparison with the estimated SE of the estimates. The CV of the GAM method estimate is just over half the CV of the traditional method. This increase in precision is not unexpected, given the substantial spatial and temporal trend in observed egg densities within the survey region. The GAM method is able to model this trend relatively parsimoniously using smoothers whereas the traditional method model's spatial trend much less parsimoniously: it effectively models the spatial trend via a two-dimensional step function with a step (and hence, a parameter) at every half-degree block.

In contrast with the above results, if we take egg count as the response, we obtain a much lower estimate. Egg densities of up to 800 were recorded, and these tended to have high conversion factors (Fig. 9*b*), which means that volume of the subsample taken was small. If the count model is fitted here, these high densities have relatively low weights because the actual counts in the subsamples were low (Fig. 9*a*). The resulting egg production estimate for 1995 is 43% lower than that obtained from the density model.

Discussion

GAM-based AEPM requires sampling to span the spawning area adequately throughout the spawning period. In cases of less adequate survey designs, the success of the methods depends on the availability of historical data for constraining the spatial distribution. Incorporating historical knowledge of the spatiotemporal distribution of Atlantic mackerel in the form of constraints, namely start and finish

Fig. 7. Estimated egg production curves for Atlantic mackerel in 1995 using the density model (smooth curve) and the corresponding curve from the traditional method (piecewise linear curve).



dates and spatial boundaries of spawning, we can reliably extrapolate beyond the sampled region. This is illustrated in our example for the predicted Atlantic mackerel egg densities early in the season in 1995 (29 February and 20 March in Fig. 6). The GAM method has successfully extrapolated for the whole survey area in that time, when there were few sampling points and these were concentrated towards the south along the 200-m contour line (Fig. 3). Sampling effort can be concentrated on time points and locations where high abundances are expected. The traditional AEPM is less sensitive to confounding of sampling in space and time within a single period, but it is equally important to determine the boundaries of the spawning area, and with the traditional method, all extrapolation is essentially ad hoc whereas with the GAM method, it is model based.

The GAM-based AEPM in our example yields a much more precise estimate and provides a variance estimate that contains all relevant components of variation. In contrast, the traditional method neglects the component of variance due to estimation of the shape of the egg production curve. Viewed in terms of survey effort required to achieve a given precision, the improved precision of the GAM method estimates would translate into a substantial reduction in survey costs. The survey design could be improved to better suit the GAM method, but the exact requirements and feasibility of optimal survey designs for the GAM-based AEPM deserve further investigation. In addition to improving precision, it is clear from our example that the GAM method provides information on the relationship between the response and covariates. Not surprisingly, the most important relationship is between date, which is a proxy for water temperature and other physical covariates, and egg density. This information on covariate–response relationships could in principle be used to improve survey design.

As a by-product, the GAM-based AEPM is able to model complex trends in density with respect to space, time, and other covariates, without ad hoc assumptions about the form of the trends. In addition, the method provides information on the nature of these trends with respect to a wide variety

© 1998 NRC Canada

Fig. 8. Estimated smoothers of the covariates (*a*) date, (*b*) cdist, distance (nautical miles) to the 200-m contour line (negative if depth > 200), (*c*) gdist, distance (nautical miles) along the 200-m contour line, and (*d*) log(depth), log(bottom depth (m)), fitted in the density model (response is density). The smoother indicates the partial effect of date on the linear predictor, i.e., the effect given that the other covariates are in the model. Zero on the vertical axis corresponds to no effect of the covariates fitted in the GAM. The covariates are centred, i.e., zero corresponds to the mean of the covariate. The broken lines correspond to confidence bands.

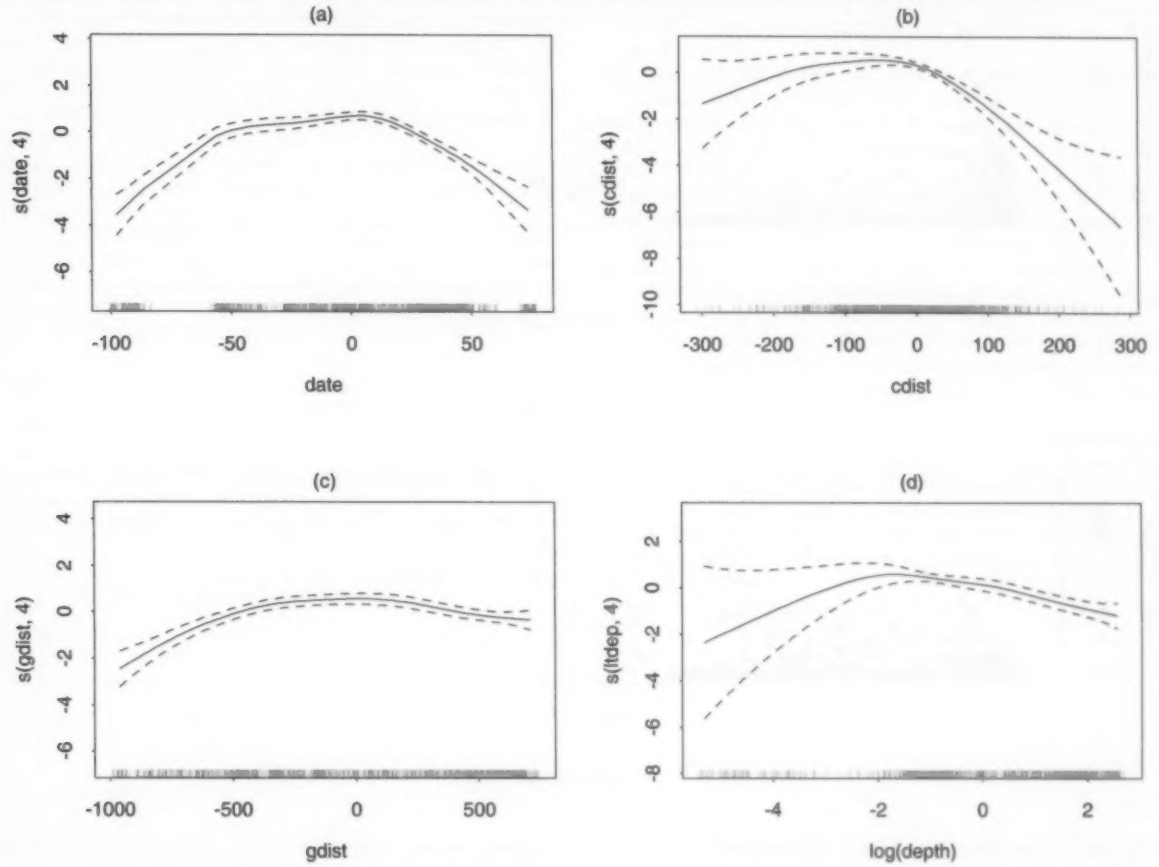


Table 1. Comparison of estimates of total egg production in 1995 ($\hat{E}_a$) from the GAM method using the density model and the traditional method.

	GAM method (density model)	Traditional method
$\hat{E}_a \times 10^{-15}$	1.49	1.48
SE	0.10	0.17
CV	6.9	11.5

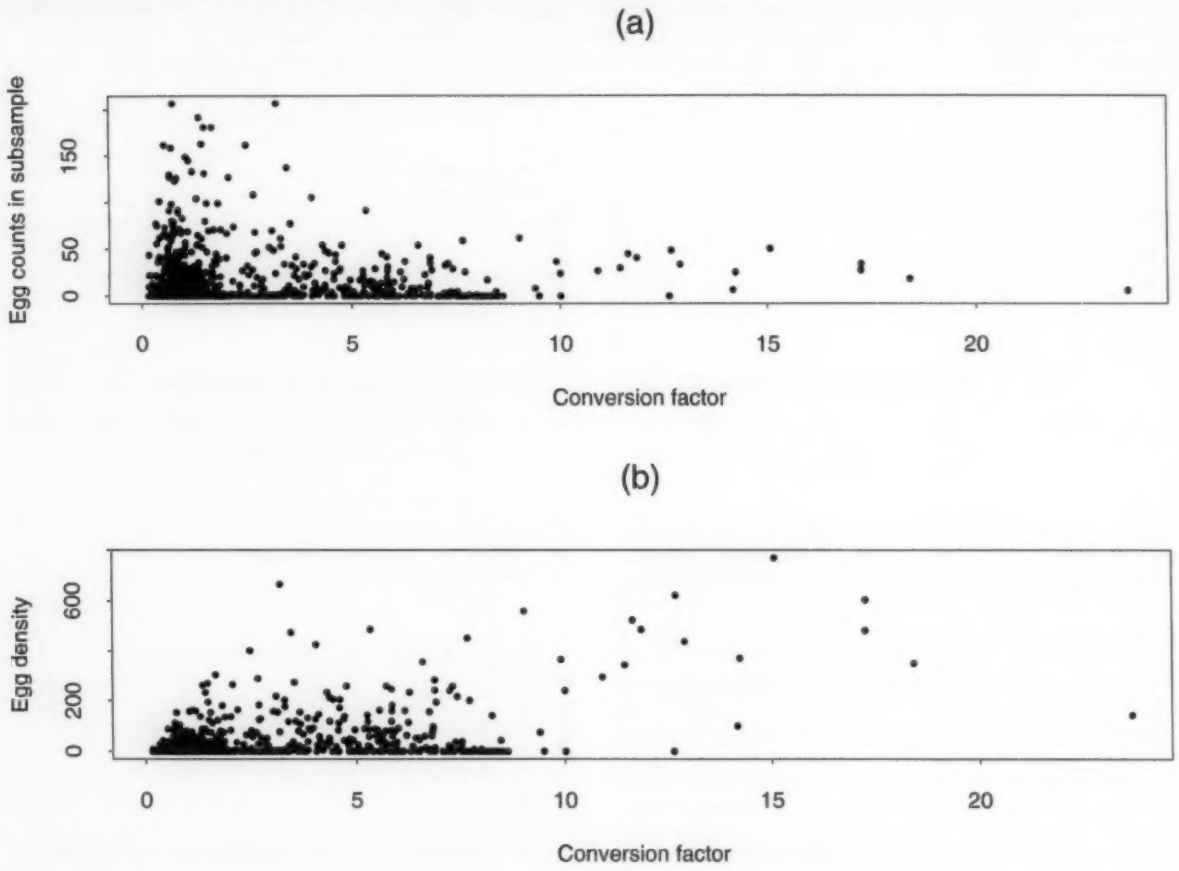
of covariates, and at a resolution that is likely to provide useful insights into the underlying mechanisms driving spawning distribution. In the traditional method, only substantial changes in the distribution with time are visible, and only between a few time points.

A notable feature of the egg production curve estimated using the GAM method shown (Fig. 7) is its relative insensitivity to the assumed start and end times for spawning (provided the times do not span too narrow a period). When egg production is low early in the season, the GAM-estimated egg production curve remains low until substantial spawning is observed. When spawning starts early, the GAM curve is able to respond appropriately. The traditional method estimate, on the other hand, is completely unable to respond to what evidence there may be in the data for onset and ending of spawning; these limits are fixed by assumption, and changing them can have a substantial effect on the estimates, independently of the data.

The attractions of the traditional method are its simplicity and its supposedly assumption-free nature. While it is true that the point estimates of egg production for a given short period in time from the traditional method involve few assumptions, fairly strong assumptions are used in estimating the egg production curve as a function of time (start and end times for spawning and the piecewise linear shape of the curve are assumed without reference to the data), and ad hoc procedures are required to fill in unsampled rectangles. It is also true that the GAM method involves substantially more modelling than the traditional method, and like any powerful tool, it could give misleading results if used inappropriately. As illustrated in the Atlantic mackerel example, care needs to be taken when choosing the appropriate response variable

© 1998 NRC Canada

Fig. 9. (*a*) Atlantic mackerel egg counts in subsample versus the conversion factor; (*b*) Atlantic mackerel egg density versus the conversion factor, which converts counts in the subsample to egg density.



in the model. An attraction of the GAM method is that it allows the data to determine the model. This is not true for the traditional method.

We considered two choices for response variable: egg count and egg density. When egg count is used, it is important to check whether the conversion factor depends on egg density. If, as here, it does, strong negative bias in the egg production estimate can be introduced. Similar bias has been observed by others, although the issue of bias correction has received little attention in the literature. It seems likely that the bias observed by Swartzman et al. (1992) was due to the bias described above. We advise in such circumstances the use of density as a response.

If there is still unmodelled spatial correlation, this could be due to the fact that the smoothed functions of the covariates cannot fully explain the similarities between egg densities in neighbouring survey rectangles, either because a potentially important covariate has not been measured or because of more direct influences such as social behaviour. In our example, such remaining spatial correlation is negligible (Fig. 5). It is in principle possible to account for this unmodelled spatial correlation by introducing an autocovariate, i.e., an extra covariate depending on egg density in surrounding survey rectangles (Besag 1974; Augustin et al. 1996). We do not pursue this here.

The application of the GAM method illustrated here shows it to be a viable alternative to the traditional method. It is an alternative that has many desirable features not available with the traditional method, not the least of which is a potential for a substantial saving in survey costs. With surveys designed specifically with a GAM method analysis in mind, the potential gains can increase further.

Acknowledgements

This research was supported by the Commission of the European Communities Directorate General for Fisheries (DG XIV) project No. 94/107. We thank our colleagues from the various countries involved in collection of the data: M. De Fatima Borges, L. Valdés, A. Sola, J. Nichols, D. Schnack, A. Eltink, S.A. Iversen, J. Molloy, J. McMillan, and L. Motos Izeta. The digitized bathometry data set DBDB5 was compiled by the U.S. Naval Oceanographic Office and made available by the British Oceanographic Data Centre.

© 1998 NRC Canada

References

Anonymous. 1994. Spawning biology, distribution and abundance of mackerel, *Scomber scombrus*, and horse mackerel, *Trachurus trachurus*, in the North East Atlantic. A final report to the Directorate General for Fisheries (DG XIV) of the Commission of the European Communities, Luxembourg. Project No. MA2436.

Anonymous. 1996. Report of the working group on mackerel and horse mackerel egg surveys, March 1996. ICES CM 1996/H:2.

Augustin, N.H., Mugglestone, M.A., and Buckland, S.T. 1996. An autologistic model for the spatial distribution of wildlife. J. Appl. Ecol. **33**: 339–347.

Besag, J. 1974. Spatial interaction and the statistical analysis of lattice systems (with discussion). J. R. Stat. Soc. Ser. B (Methodol.), **36**: 192–236.

Borchers, D.L., Augustin, N.H., and Buckland, S.T. 1997*a*. Spatio-temporal model development to improve annual egg production assessments of mackerel/horse mackerel. A final report to the Directorate General for Fisheries (DG XIV) of the Commission of the European Communities, Luxembourg. Project No. 94/107.

Borchers, D.L., Buckland, S.T., Priede, I.G., and Ahmadi, S. 1997*b*. Improving the precision of the daily egg production method using generalized additive models. Can. J. Fish. Aquat. Sci. **54**: 2727–2742.

Deriso, R.B., Barnes, J.T., Jacobson, L.D., and Arenas, P.R. 1996. Catch-at-age analysis for Pacific sardine (*Sarinops sagax*), 1983–1995. Calif. Coop. Oceanic Fish. Invest. Rep. **37**: 175–187.

Efron, B., and Tibshirani, R.J. 1993. An introduction to the bootstrap. Chapman and Hall, London, U.K.

Gunderson, D.R. 1993. Surveys of fisheries resources. John Wiley & Sons, Inc., New York.

Hastie, T., and Tibshirani, R.J. 1990. Generalized additive models. Chapman and Hall, London, U.K.

Maravelias, C.D., and Reid, D.G. 1997. Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models. Mar. Ecol. Prog. Ser. **147**: 1–9.

McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. Chapman and Hall, London, U.K.

Swartzman, G. 1997. Analysis of the summer distribution of fish schools in the Pacific Eastern Boundary Current. ICES J. Mar. Sci. **54**: 105–116.

Swartzman, G., Huang, C.H., and Kaluzny, S. 1992. Spatial analysis of Bering sea groundfish survey data using generalized additive models. Can. J. Fish. Aquat. Sci. **49**: 1366–1378.

Swartzman, G., Stuetzle, W., Kulman, K., and Powojowski, M. 1994. Relating the distribution of pollock schools in the Bering Sea to environmental factors. ICES J. Mar. Sci. **51**: 481–492.

Swartzman, G., Silverman, E., and Williamson, N. 1995. Relating trends in walleye pollock *(Theragra chalcogramma)* abundance in the Bering Sea to environmental factors. Can. J. Fish. Aquat. Sci. **52**: 369–380.

Welch, D.W., Chigirinsky, A.I., and Ishida, Y. 1995. Upper thermal limits on the oceanic distribution of Pacific salmon (*Oncorhynchus* spp.) in the spring. Can. J. Fish. Aquat. Sci. **52**: 489–503.

Wood, S.N., and Horwood, J.W. 1995. Spatial distribution functions and abundances inferred from sparse noisy plankton data: an application of constrained thin-plate splines. J. Plankton Res. **17**: 1189–1208.

© 1998 NRC Canada

Modeling the effects of fish migration on bias and variance in area-swept estimates of biomass: a vector-based approach

Murdoch K. McAllister

Abstract: Estimates of fish abundance from trawl and acoustic surveys are typically imprecise and may often be biased because of uncontrollable factors such as fish migration. In this paper, I present a model for the bias in area-swept biomass estimates when fish migration occurs as the survey is conducted. Bias in acoustic and trawl survey biomass estimates is treated as a function of the direction and speed of the vessel and the fish in each survey transect and results mainly from distortions in the observed area across fish aggregations. I use the model to evaluate the magnitude and direction of bias and interannual variability in biomass estimates from fish migration in systematic transect survey designs. For even relatively low fish migration velocities (<0.5 m/s), bias in estimated fish biomass can be very large (>500%). Furthermore, relatively small interannual variability in fish migration rates and vessel speeds (e.g., CV = 0.1 for each) can result in very large interannual error variability in biomass estimates (e.g., CV > 0.5). Designs with the least bias and variance in biomass estimates had the fastest vessel speeds along transects, more survey vessels, shorter transects, and transects aligned roughly parallel to the direction of fish migration.

Résumé : Les estimations de l'abondance des poissons fournies par les campagnes de chalutage scientifique et de détection acoustique sont généralement imprécises, et peuvent souvent être biaisées par des facteurs incontrôlables comme les migrations. Je présente ici un modèle du biais qui marque les estimations de la biomasse par balayage de zone quand la migration se produit au cours du relevé. Le biais des estimations de la biomasse fournies par les campagnes de chalutage et de détection acoustique est traité comme une fonction de la direction et de la vitesse du bateau et des poissons dans chaque transect suivi, et provient principalement de distorsions dans la zone observée entre les divers regroupements de poissons. Je me sers du modèle pour évaluer l'ampleur et la direction du biais et la variabilité interannuelle des estimations de la biomasse causées par les migrations dans les relevés systématiques sur transects. Pour des vitesses de migration même relativement faibles (< 0,5 m/s), le biais des estimations de la biomasse peut être très grand (> 500 %). En outre, une variabilité interannuelle relativement faible des vitesses de migration des poissons et de la vitesse du bateau (p.ex, CV = 0,1 dans chaque cas) peut se traduire par une très grande variabilité interannuelle des estimations de la biomasse (p.ex., CV > 0,5). Les relevés donnant le moins de biais et de variance dans les estimations de la biomasse présentaient les caractéristiques suivantes : vitesses plus élevées des bateaux sur les transects, plus grand nombre de bateaux dans les relevés, transects plus courts, et transects grossièrement alignés sur la direction de la migration des poissons.

[Traduit par la Rédaction]

Introduction

It is well known that many fish species migrate at some point in their life history (Harden Jones 1968). Acoustic and trawl surveys that provide area-swept biomass estimates are often applied to such populations (MacLennan and Simmonds 1992; Gunderson 1993). A common feature of the design of such surveys is to ensure that the survey area includes the entire population (Godø 1989; Simmonds et al. 1992). But even when this condition is met, a large horizontal movement of fish within the survey area (or "migration") can bias biomass estimates. Furthermore, interannual variability in migration velocities and (or) interannual variability in the rate at which survey vessels proceed over the survey area can increase the interannual variability in estimates of fish abundance (Byrne et al. 1981; MacLennan and Simmonds 1992).

There has been relatively little attention given to the amount of bias or error variation that can be caused by the interaction of fish movement with survey protocol. MacLennan and Simmonds (1992) introduced bias correction factors for the effects of migration on biomass estimates and suggested how survey transects can be aligned with respect to the direction of fish migration in order to minimize bias.

In this paper, I provide an alternative to MacLennan and Simmonds' (1992) formulation for bias in acoustic surveys when migration occurs that has improved conceptual consistency and generality. I extend the new formulation so that it can also be applied to trawl surveys. The formulation is used

Received July 10, 1997. Accepted August 26, 1998.
J14105

M.K. McAllister.[1] Fisheries Research Institute, University of Washington, Box 357980, Seattle, WA 98195-7980, U.S.A.

[1]Present address: Renewable Resources Assessment Group, T.H. Huxley School of Environment, Earth Sciences and Engineering, Imperial College, 8 Princes Gardens, London, SW7 1NA, U.K. e-mail: m.mcallister@ic.ac.uk

© 1998 NRC Canada

to evaluate the potential effects of fish migration and survey design on bias in biomass estimates. Interannual variability in biomass estimates from interannual variability in fish migration and vessel speeds was estimated using Monte Carlo simulation. Because results for trawl surveys are similar to those for acoustic surveys (McAllister 1995), results for acoustic surveys only are shown.

This article is organized as follows. The first section points out various shortcomings of an earlier model for bias from migration in fishery surveys. The second section presents an alternative model and the equations are derived to model bias from fish migration in acoustic surveys. The third section provides an extension of the model to trawl survey estimates of abundance. The fourth section evaluates the potential bias and variability in biomass estimates from migration in a variety of alternative survey designs.

Modeling bias and variability from migration in area-swept biomass estimates

Modeling bias in acoustic biomass estimates

MacLennan and Simmonds' (1992) approach

Area-swept estimates of fish biomass in acoustic and trawl surveys are obtained by multiplying the geographic area surveyed by the estimated mean fish density. Among other things, these estimators assume that there is no net directional movement of fish. MacLennan and Simmonds (1992) pointed out that fish migration can cause the "effective" area surveyed to differ from the geographical area surveyed. For example, if fish are migrating against the vessel's direction as it proceeds between successive transects, the geographical area surveyed (i.e., the area used in the estimate) will be smaller than the actual area of the population that is sampled (i.e., the effective area) and the estimated biomass will be negatively biased.

In contrast with MacLennan and Simmonds (1992), I define movement vectors relative to an x,y coordinate. The transects considered are arrayed parallel to the y-axis. Let $v_{v,x}$, $v_{v,y}$, $v_{f,x}$, and $v_{f,y}$ be the velocity vectors of the vessel and fish parallel to the x- and y-axes, respectively. For example, $v_{f,y}$ is positive if the net movement of fish along the y-axis is positive. MacLennan and Simmonds (1992) suggested that the expected value for the biomass estimate $E(\hat{B})$ when fish migration occurs is given by

$$(1) \qquad E(\hat{B}) = B\left(1 + \frac{v_{f,x}}{v_{v,x}}\right)$$

where B is the true biomass. This equation appears to be sensible. For example, if the direction of fish migration is against the direction of the survey vessels, $v_{v,x}$ and $v_{f,x}$ will have opposite signs, and the expected value for the estimated biomass will be smaller than the true value, as one would expect.

However, eq. 1 has anomalous properties under various limiting conditions. First, $E(\hat{B}) = 0$ if $v_{v,x} = -v_{f,x}$ (the expected value of the estimate is zero if the fish and vessel are moving in opposite directions but at equal velocity). Second, $E(\hat{B}) = 2B$ if $v_{f,x} = v_{v,x}$ (the expected value of the estimate is twice the actual value if the fish and vessel are moving in the same direction at equal velocity). Third, $E(\hat{B}) < 0$ if $(v_{f,x}/v_{v,x}) < -1$ (the expected value of the estimate is negative if the fish and vessel are moving in opposite directions and the velocity of the vessel is less than that of the fish). Fourth, $E(\hat{B})$ approaches negative or positive infinity as $v_{v,x}$ approaches zero, depending on whether $v_{v,x}$ is negative or positive.

Proposed formulation for bias from migration in acoustic biomass estimates

In this section, I present an alternative to MacLennan and Simmonds' (1992) formulation for bias from migration. In contrast with theirs, I formulate estimated biomass as a function of the true biomass and the speed and direction (velocity vectors) of the survey vessel and fish in each of the transects in a survey (McAllister 1995, appendix E). The new formulation makes the following assumptions. "Fish aggregation" refers to the summation of all fish aggregations within the area surveyed. The estimated geographic area surveyed is unbiased. Fish densities estimated at each point along acoustic transects are unbiased by fish movement (MacLennan and Simmonds 1992; Aglen 1994). In contrast, the observed area of the fish aggregation may be biased by fish movement and thereby also the estimate of mean density in a transect and across all transects. Take, for example, a vessel following an aggregation as it moves between transects. The observed distance across the aggregation on the axis perpendicular to the transects will be larger than the actual distance. Therefore the observed area of the aggregation will be larger than the actual area and the estimated mean density of fish in the survey area will be positively biased. The observed distances across the fish aggregation and the observed fish density in the survey area can be expressed as functions of vessel and fish velocity on each survey transect, among other things. Thus, I have formulated below an expression for estimated fish density as a function of the velocity vectors of the fish and the vessel in each survey transect.

To start the formulation, fish density in an area, D, is sometimes estimated by finding the mean density across all transects (assuming that they are of equal length or have the same number of sampling units (MacLennan and Simmonds 1992)):

$$(2) \qquad \hat{D} = \frac{1}{T}\sum_{t=1}^{T}\hat{D}_t$$

where $\hat{D}$ is the estimated mean density of fish in the survey area, $\hat{D}_t$ is the estimated density in transect t, and T is the number of transects. The formulation makes the following additional assumptions: $\hat{D}_t$ is a random variable that depends on the initial position of the fish aggregation as the survey begins, $\hat{D}_t$ is a function of the velocity vectors of the fish and the direction of movement of the vessel along a transect, the fish aggregation is rectangular in shape with its sides aligned parallel to the x and y directions, and fish remain within the survey area during the survey.

In order to evaluate the bias in $\hat{D}_t$ that results from the movement of fish and the survey vessel, we need an expres-

© 1998 NRC Canada

sion for the expected value for $\hat{D}_t$, $E(\hat{D}_t)$, the mean value of $\hat{D}_t$ across all potential spatial arrays of the fish aggregation in the survey area. The expectation of $\hat{D}_t$ can be formulated as the conditional expectation

$$(3) \quad E(\hat{D}_t) = E(\hat{D}_t | \hat{D}_t \neq 0) P(\hat{D}_t \neq 0)$$

where $E(\hat{D}_t | \hat{D}_t \neq 0)$ is the expected value of $\hat{D}_t$, given that $\hat{D}_t$ does not equal zero, and $P(\hat{D}_t \neq 0)$ is the probability that $\hat{D}_t \neq 0$. The derivation of these two components in eq. 3 is based on the expected observed distance across the fish aggregation versus actual distances across the fish aggregation (Appendix). Below, I provide the results of the derivation.

$E(\hat{D}_t | \hat{D}_t \neq 0)$ can be expressed by

$$(4a) \quad E(\hat{D}_t | \hat{D}_t \neq 0) = [\text{true fish density on transect}] \times [\text{bias factor (vessel and fish movement)}]$$

where

$$(4b) \quad \text{Bias factor (vessel and fish movement)} = r_{y,t} = \frac{\left|\text{velocity of vessel on } y \text{ axis}\right|}{\left|\begin{array}{l}\text{velocity of vessel} \\ \text{relative to fish on } y \text{ axis}\end{array}\right| + \left|\text{velocity of fish on } x \text{ axis}\right| \times (\text{aggregation shape correction factor})}.$$

Thus:

$$(4c) \quad E(\hat{D}_t | \hat{D}_t \neq 0) = D_t r_{y,t} = D_f \frac{\bar{d}_y^f}{L_\tau} \frac{\left|v_{v,y,t}\right|}{\left|v_{v,y,t} - v_{f,y}\right| + \left|v_{f,x}\right| \frac{\bar{d}_y^f}{\bar{d}_x^f}}$$

where D_f is the mean density of fish within the aggregation, $\bar{d}_x^f$ and $\bar{d}_y^f$ are the mean distances across the fish aggregation in the x and y directions, L_t is the length of transect t, $v_{v,y,t}$ is the velocity vector of the vessel in the y direction on transect t, and all other terms are defined above (see Appendix). It can be easily seen that $E(\hat{D}_t | \hat{D}_t \neq 0)$ is unbiased if the velocity vectors of the fish, $v_{f,x}$ and $v_{f,y}$, are both zero, i.e., $r_{y,t}$ will be equal to the denominator and $r_{y,t}$ will cancel out leaving an expression for the true density of fish on the transect:

$$(4d) \quad E(\hat{D}_t | \hat{D}_t \neq 0) = D_f \frac{\bar{d}_y^f}{L_\tau} = D_t.$$

It can also be seen that if fish and the vessel are moving in the same direction, $|v_{f,y}| < 2|v_{v,y,t}|$, and $v_{f,x} = 0$, then the denominator of $r_{y,t}$ will be smaller than the numerator and $E(\hat{D}_t | \hat{D}_t \neq 0)$ will be positively biased. If fish and the vessel are moving in opposite directions along the transect, then the denominator of $r_{y,t}$ will be larger than the numerator and negative bias will result.

If there is movement of fish in the x direction, $v_{f,x}$ will be nonzero and the value for the denominator of $r_{y,t}$ will increase and $E(\hat{D}_t | \hat{D}_t \neq 0)$ will decrease. Movement of fish in the x direction can cause the vessel to cross one of the corners of the aggregation, a distance on the y-axis less than $\bar{d}_y^f$. Thus the density D_t may be underestimated because the estimate depends on the observed distance across the fish on the y-axis (Appendix). Finally, if the ratio $\bar{d}_y^f / \bar{d}_x^f$ is larger than 1, then there is a higher likelihood that the vessel will cross a corner of the aggregation and not the full distance on the y-axis, $\bar{d}_y^f$ (Fig. 1). This will tend to increase the denominator of $r_{y,t}$ and lower $E(\hat{D}_t | \hat{D}_t \neq 0)$. Thus, the expression for $E(\hat{D}_t | \hat{D}_t \neq 0)$ is intuitive and sensible.

The term $P(\hat{D}_t \neq 0)$ in eq. 3 can be expressed by

$$(5a) \quad P(\hat{D}_t \neq 0) = \frac{\bar{d}_x^f}{W} \frac{\left|v_{v,x,t}\right|}{\left|v_{v,x,t} - v_{f,x}\right|}$$

where W is the width of the survey area, $v_{v,x,t}$ is the velocity of the vessel in the x direction on transect t, and $0 \leq P(\hat{D}_t \neq 0) \leq 1$ (Appendix). It can be seen that when $v_{f,x} = 0$ the second term on the right-hand side (term 2) cancels and $P(\hat{D}_t \neq 0)$ equals the fraction of the distance in the x direction across the survey area that is covered by fish, an intuitive result. If the vessel and fish are traveling in the same direction as the vessel proceeds between transects, the denominator of term 2 becomes smaller than the numerator and $P(\hat{D}_t \neq 0)$ increases; $P(\hat{D}_t \neq 0)$ decreases if the opposite is the case. Furthermore, because $P(\hat{D}_t \neq 0)$ is a probability, the following must hold:

$$(5b) \quad 0 \leq P(\hat{D}_t \neq 0) \leq 1, \frac{\bar{d}_x^f \left|v_{v,x,t}\right|}{W \left|v_{v,x,t} - v_{f,x}\right|} \leq 1,$$

$$\text{and} \frac{\left|v_{v,x,t}\right|}{\left|v_{v,x,t} - v_{f,x}\right|} \leq \frac{W}{\bar{d}_x^f}.$$

These inequalities are used in eq. 7 below.

The expected estimate of biomass in the survey area can be expressed as a function of the geographic area surveyed and mean expected estimated density of fish across all transects:

$$(6) \quad E(\hat{B}) = A \cdot E(\hat{D}) = \frac{A}{T} \sum_{t=1}^{T} E(\hat{D}_t)$$

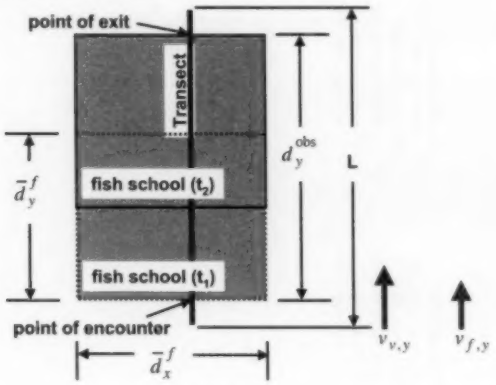
where A is the area surveyed ($A \approx W\bar{L}$ where $\bar{L}$ is the average transect length) and T is the number of transects. Using eqs. 3, 4*a*, 4*b*, 4*c*, 5, and 6, it can be shown that (McAllister 1995, appendix E)

$$(7a) \quad E(\hat{B}) = \frac{B}{T} \sum_{t=1}^{T} r_{x,t} r_{y,t}$$

where

© 1998 NRC Canada

Fig. 1. Schematic diagram of a fish aggregation as it would appear to a survey vessel moving along a transect when fish move in the same direction as the vessel along the transect. See text for explanation.



$$(7b)\quad r_{y,t} = \frac{\left|v_{v,y,t}\right|}{\left|v_{v,y,t} - v_{f,y}\right| + \left|v_{f,x}\right|\dfrac{\bar{d}_y^f}{\bar{d}_x^f}}$$

$$(7c)\quad r_{x,t} = \frac{\left|v_{v,x,t}\right|}{\left|v_{v,x,t} - v_{f,x}\right|}$$

$$(7d)\quad r_{x,t} \le \frac{W}{\bar{d}_x^f} \text{ and } r_{y,t} \le \frac{L_t}{\bar{d}_y^f} \text{ or } r_{x,t} \le r_{\max,x}$$

$$\text{and } r_{y,t} \le r_{\max,y} \text{ and } r_{\max,x} = \frac{W}{\bar{d}_x^f} \text{ and } r_{\max,y} = \frac{\bar{L}}{\bar{d}_y^f}.$$

Equation 7*b* reflects the quotient for velocity terms in the equation for $E(\hat{D}_t | \hat{D}_t \neq 0)$ (eq. 4*c*). Equation 7*c* reflects the quotient for velocity terms in the equation for $P(\hat{D}_t \neq 0)$ (eq. 5*a*) The inequalities in eq. 7*d* reflect the constraint that the equations apply only to situations in which the fish remain within the survey area during the survey. The inequalities also suggest the limit for the maximum potential bias that can occur as a result of fish migration during the survey.

It is instructive to further describe some of the properties of eq. 7. For a situation in which $v_{f,x} \neq 0$ but $v_{f,y} = 0$ and $\bar{d}_x^f = \bar{d}_y^f$, eq. 7 reduces to

$$(7e)\quad E(\hat{B}) = B\frac{\left|v_{v,y}\right|}{\left|v_{v,y}\right| + \left|v_{f,x}\right|} \cdot \frac{\left|v_{v,x}\right|}{\left|v_{v,x} - v_{f,x}\right|}.$$

Note that if fish are moving in the direction opposite to that of the vessel but at the same speed, $E(\hat{B})$ is some value greater than zero but less than or equal to $0.5B$, a sensible result. Negative biomass estimates cannot be obtained from eq. 7 and conceptually sensible results are obtainable should $v_{v,x}$ approach zero. If fish migration velocity approaches that of the survey vessel in the x direction, the estimated biomass approaches $B \cdot r_{\max,x}$ (eq. 7*d*). This latter result is sensible, since if the fish and the vessel are moving in the same direction at the same speed, a small school will appear as a large school and estimated biomass will have a large positive bias. An inconvenience is that values for $r_{\max,x}$ and $r_{\max,y}$ (i.e., $r_{\max}$) need to be known in order to specify the maximum possible bias from migration. For the purposes of estimating bias, it can usually be assumed, however, that these ratios are large (e.g., $r_{\max,y} > 2$).

Bias from migration in area-swept estimates in trawl surveys

The assumption that the estimated density at each point along a transect is not biased by fish movement is untenable for trawl surveys. This is because the density at each sampling station along a transect is estimated by dividing the mass of the catch in each haul by the area swept by the haul. This calculation assumes that there is no migration. However, the catch and density estimate per haul may depend on the direction and speed of fish migration and the survey vessel as it hauls the net. Take, for example, a vessel hauling its net in the direction opposite to fish migration. The net will encounter more fish during the haul and potentially catch more fish than if there were no migration, and estimated density may be too large. Therefore, the equation used for acoustic biomass estimates (eq. 7) is not appropriate for trawl estimates of abundance. McAllister (1995, appendix F) derived an expression that expresses the density in a given haul as a function of the velocity vectors of the vessel and the fish in the transect. It is shown that the expected estimate of biomass as a function of the velocity vectors of the fish and the vessel and the true biomass in the survey area can be approximated by

$$(8a)\quad E(\hat{B}) \cong \frac{B}{T}\sum_{t=1}^{T}\left(r_{x,t} r_{y,t} r_{y,h,t}^{-1}\right)$$

where

$$(8b)\quad r_{y,h,t} = \frac{\left|v_{y,h,t}\right|}{\left|v_{y,h,t} - v_{f,y}\right|}$$

$$(8c)\quad r_{y,t} = \frac{\left|v_{v,y,t}\right|}{\left|v_{v,y,t} - v_{f,y}\right| + \left|v_{f,x}\right|\dfrac{\bar{d}_y^f}{\bar{d}_x^f}}$$

$$(8d)\quad r_{x,t} = \frac{\left|v_{v,x,t}\right|}{\left|v_{v,x,t} - v_{f,x}\right|},$$

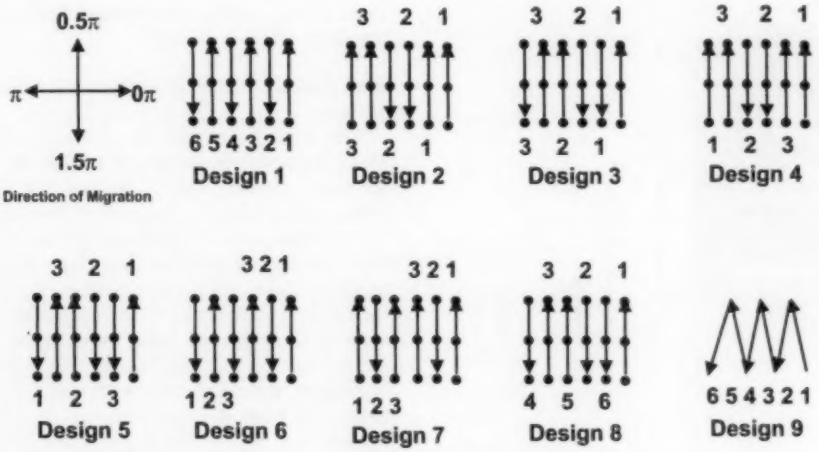
$v_{y,h,t}$ is the velocity vector of the haul in the y direction (the velocity vector of the haul in the x direction cancels out; see McAllister 1995, appendix F), $v_{v,x,t}$ and $v_{v,y,t}$ are the velocity vectors of the vessel in the x and y directions on transect t, and

$$(8e)\quad r_{x,t} \le \frac{W}{\bar{d}_x^f} \text{ and } r_{y,t} \le \frac{L_t}{\bar{d}_y^f}$$

where W is the width of the survey area, L_t is the length of transect t, $\bar{d}_x^f$ is the distance across the fish in the x direction, and $\bar{d}_y^f$ is the distance across the fish in the y direction; $r_{y,h,t}^{-1}$ is the multiplier that reflects the bias in the density estimate

© 1998 NRC Canada

Fig. 2. Diagram showing nine different survey protocols and the coordinates for the direction of migration with respect to survey design. The numbers on the top and bottom of each set of arrows show the order of execution of transects for each of the vessels. The arrows show the direction that the vessel travels along the transect. The dots show the position of sampling stations in the trawl designs.



in individual hauls in each transect, and $r_{x,t}$ and $r_{y,t}$ are as they were for the acoustic estimator in eq. 7.

In most trawl surveys, vessel velocity is greater than fish velocity when both move in the same direction and the net vessel speed along a transect is similar to the towing speed. Therefore, the bias in the observed size of fish aggregations caused by migration along the transects may sometimes cancel out the bias in observed density at each sampling station along the transect. This suggests that bias from fish migration in trawl surveys may be lowered by aligning transects parallel to the direction of fish migration so that cross-transect migration speed ($v_{f,x}$) is zero and $r_{x,t} = 1$.

Evaluating the biases in biomass estimates from migration in alternative surveys

The effects of various aspects of survey design on biases in biomass estimates from migration were calculated using eq. 7 and the assumption that the x and y coordinates of the fish aggregation are equal (i.e., $\bar{d}_x^f = \bar{d}_y^f$ in eq. 7*b*). The designs evaluated had features similar to the systematic trawl and acoustic survey designs in the eastern Bering Sea (Gunderson 1993; Karp and Walters 1994) and were deliberately simplistic to facilitate the illustration of the potential effects of migration on survey biomass estimates. Thus the designs had transects of fixed length that were equally spaced (see below and Fig. 2). The baseline design considered had one survey vessel. There were six parallel transects, each 73.6 km (40 nautical miles) long and 36.8 km (20 nautical miles) apart. In the trawl designs, sampling stations were set 36.8 km apart. The transects were numbered from 1 to 6 going right to left. The vessel proceeded up the first, down the second, and so on. The vessel proceeded at an average velocity of 2.06 m/s (4 kn). As implied in eq. 7 the expected biases were calculated for each transect given the velocity vectors in each transect in the design and then averaged.

A wide range of fish velocities were considered (up to 3 m/s). Since sustained migration velocities of marine fishes with lengths between 10 and 100 cm range between two and three body lengths per second (Harden Jones 1968), the extreme velocities considered are not impossible. Such high velocities are also conceivable when ocean currents act to enhance fish migration velocities. For simplicity, most results are presented for situations in which fish movement is either perpendicular or parallel to survey transects. Estimation of biases also requires values for the ratios of maximum observable aggregation width to the actual width, r_{max}. The baseline value chosen for these ratios was 10. This value reflects fish aggregation dimensions that are as small as 1/10 the length of a transect.

The effect of the following factors on potential biases were evaluated: (*i*) fish migration directions and velocities using the baseline design, (*ii*) assumed ratio of maximum observable aggregation width to actual width (r_{max}), (*iii*) length of survey transects, (*iv*) number of transects used in the survey, (*v*) mean vessel velocities along transects, (*vi*) number of survey vessels used, and (*vii*) order and direction in which the vessels proceed across survey transects (Fig. 2).

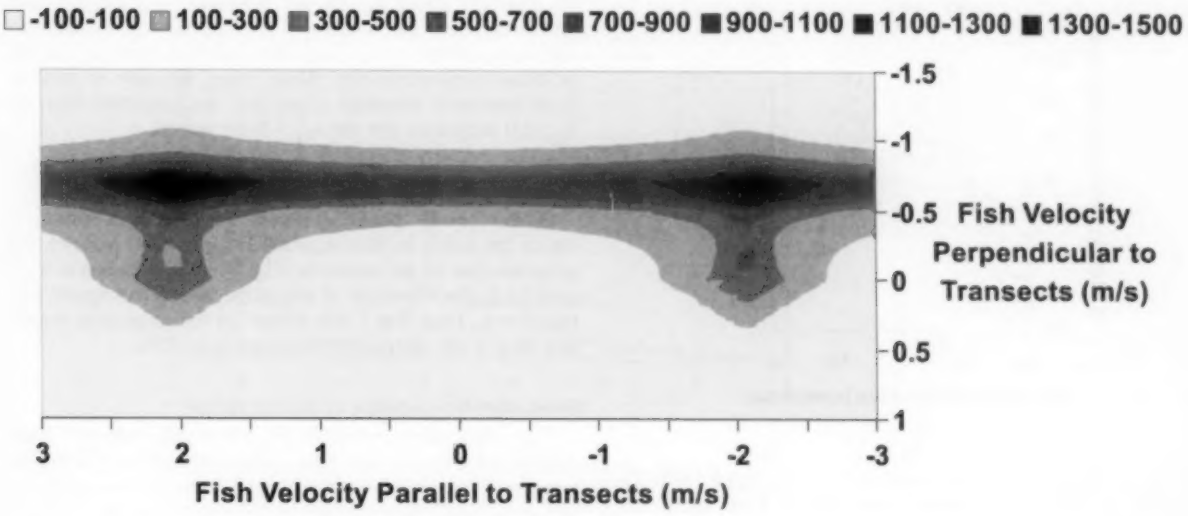
Evaluating the variability in biomass estimates from interannual variability in migration and vessel speeds

Interannual variability in migration and vessel speeds will increase the interannual variability in biomass estimates. One approach that could be taken to estimate the interannual variance in biomass estimates from the variance in the velocity vectors is the delta method (Seber 1982). However, this approach would be complicated because of the use of boundary conditions in the estimators of bias from migration (e.g., r_{max} in eq. 7). Therefore, estimates of the interannual variance in biomass estimates were obtained using Monte Carlo simulation.

The Monte Carlo procedure used assumes that mean annual velocities of fish, v_f, and vessels, v_v, are normally distributed with a constant coefficient of variation (CV) and independent:

© 1998 NRC Canada

Fig. 3. % Bias in biomass estimates as a function of fish migration speed and direction. The design has six parallel transects 20 nautical miles long and the survey vessel travels at 2.06 m/s along the transects (Fig. 2, Design 1). On odd-numbered transects, vessel velocity is positive; on even-numbered transects, vessel velocity is negative.



$$(9)\qquad \begin{aligned} v_f &\sim N(\bar{v}_f, \mathrm{CV}_f^2\,\bar{v}_f^2) \\ v_v &\sim N(\bar{v}_v, \mathrm{CV}_v^2\,\bar{v}_v^2) \end{aligned}$$

where CV_v is the across-year CV in the mean annual vessel speed along the transects, $\bar{v}_f$ is the mean across years of the annual velocity vector of the fish, $\bar{v}_v$ is the mean across years of the annual vector of the cruising speed of the vessel along a transect, and CV_f is the CV in mean annual fish migration speed. Variance from within-year sources of variability was left out, i.e., only interannual variability in velocity vectors was simulated. In each Monte Carlo replicate, a value for v_f and v_v was generated from their respective distributions. The next step was to estimate the biomass using eq. 7. The standard deviation in the biomass estimate across all Monte Carlo replicates was computed by

$$(10)\qquad \mathrm{SD}(\hat{B}) = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(\hat{B}_i - \bar{B})^2}$$

where n is the number of Monte Carlo simulations (1000), $\hat{B}_i$ is the estimate of biomass in simulation i, and $\bar{B}$ is the mean biomass across all simulations.

Because the variance and the expected value for the estimated biomass depend on the conditions assumed, it is more instructive to compute a relative measure of variability. Thus the CV in biomass estimates was used:

$$(11)\qquad \mathrm{CV}(\hat{B}) = \frac{\mathrm{SD}(\hat{B})}{\bar{B}}.$$

In each design considered, 1000 Monte Carlo replicates were used to estimate $\mathrm{CV}(\hat{B})$, $\mathrm{CV}_f = 0.1$, $\mathrm{CV}_v = 0.1$, and $\mathrm{CV}(\hat{B})$ was estimated over a range of directions of migration and migration speeds. The baseline design (Fig. 2, Design 1) was used to evaluate the sensitivity of $\mathrm{CV}(\hat{B})$ to different vessel speeds and transect lengths. Alternative protocols for traversing transects were also considered (Fig. 2).

Results

Bias in abundance estimates

Evaluation 1: direction and speed of migration

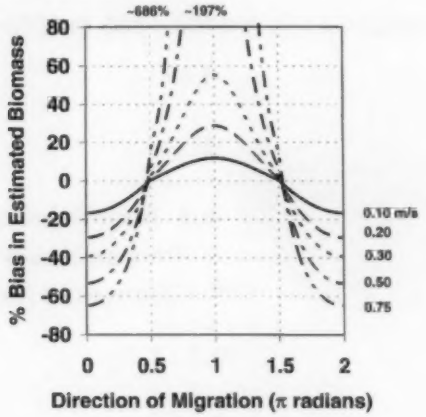
The expected biases for a large grid of fish migration directions and velocities were calculated for the baseline design (Fig. 2, Design 1). Bias was largest when fish migration vectors had components both perpendicular and parallel to the transects and the magnitudes of these components was roughly equal to the speed of the vessel across and along the transects (Fig. 3). However, this situation is unlikely to arise in most surveys because vessel speed is usually much greater than migration speed.

The migration directions that minimized bias depended to some extent on the migration speed (Fig. 4). When migration speed was less than 1 m/s, aligning transects parallel or nearly parallel to the direction of fish migration minimized bias. This was because of the compensatory effect of adding negative biases on transects going against the direction of fish migration to positive biases on transects going in the opposite direction. Such compensation did not occur when transects were aligned perpendicular to fish migration (eq. 7). As migration velocity increased, aligning transects so that the vessel moved slightly against the direction of fish migration as the vessel proceeded between transects minimized bias (Fig. 4).

Bias was very large (up to 648%) when fish migrated only perpendicular to the transects. with the same direction and speed as the vessel as it proceeded between transects

© 1998 NRC Canada

Fig. 4. % Bias in biomass estimates as a function of the direction and speed of migration. The design is the same as that in Fig. 3 and is the same in the following figures for acoustic surveys unless specified otherwise.



(Fig. 4). Migration speeds need not be very large for large biases to arise (e.g., biases were larger than 100% for –0.4 m/s > $v_{f,x}$ > –0.9 m/s). Biases decreased and became more strongly negative when fish movement was perpendicular to the transects and in the opposite direction to vessel velocity and fish velocity increased. This resulted because the apparent size of aggregations decreased when this occurred.

Evaluation 2: ratio of the maximum observable to actual aggregation size

The maximum potential bias was a function of the values for the ratio of the maximum observable to actual aggregation size, r_{max} (Fig. 5). For example, for migration perpendicular to the transects, the maximum biases were roughly proportional to these ratios, e.g., 223% if r_{max} = 5, 646% if r_{max} = 10, and 3400% if r_{max} = 100. However, for migration velocities that did not approach the vessel's velocity, biases were insensitive to the value for r_{max}.

Evaluation 3: transect length

When transect length increased, vessel velocity across transects ($v_{v,x}$) decreased. Bias from migration perpendicular to the transects ($v_{f,x}$) thus was highly sensitive to the length of the transects (Fig. 6). When transect length was doubled, the migration speed at which bias was maximum was roughly halved, e.g., from –0.7 to –0.3 m/s, and the bias at $v_{f,x}$ = –0.4 m/s increased from 101 to 737%. Bias from migration that ran parallel to the transects was insensitive to transect length, since bias in this case was not a function of vessel velocity perpendicular to the transects (eq. 7).

Evaluation 4: number of transects

Bias was not a function of the number of transects used when the number was even or when migration was perpendicular to the transects (Fig. 7). This was because the velocity of the vessel in the x and y directions was not a function of the number of transects used. However, when the number of transects was odd and fish velocity was parallel to the transects, bias became a function of the number of transects. Biases were less for negative than for positive migration velocities and larger with fewer transects. This was because the observed distance across a fish aggregation was smaller on transects going against the direction of migration than with migration, the number of the former type of transect was larger when $v_{f,y} < 0$, and the total bias was the average of biases across transects. Thus, when the ratio of odd- to even-numbered transects decreased, the expected bias for $v_{f,y} < 0$ increased and for $v_{f,y} > 0$ decreased.

Evaluation 5: vessel velocity along transects

Higher vessel speeds increased the migration speeds at which the peaks in bias occurred for migration parallel and perpendicular to the transects (Fig. 8). When transects were parallel to the direction of migration and vessel speed was raised, e.g., from 3 to 5 m/s, biases for fish migration speeds less than 1 m/s decreased by as much as 75%.

Evaluation 6: execution of survey design

Nine alternative protocols for traversing transects were considered (Fig. 2). The best protocol should minimize the expected bias for the expected ranges of migration velocities and directions in a given survey. If the direction and velocity of fish migration are known at least roughly, as they usually are, then the transects can be aligned so as to minimize bias. For example, for fish migration velocities less than 1 m/s, the designs that had the least bias had two vessels (as opposed to one), transects aligned parallel to fish migration, and twice as many transects with vessels proceeding against than with the direction of fish migration (Fig. 9, Designs 2, 4, and 7; Fig. 2). Under such conditions, absolute biases were less than 10%. However, when the direction of migration was uncertain, yet it was known that migration velocities were less than 0.5 m/s, less than 1 m/s, or between 1 and 2 m/s, the best design had two vessels each starting at opposite ends of the survey area, proceeding in opposite directions, and jumping two transects at a time or one vessel following this same protocol (Table 1, Designs 5 and 8; Fig. 2). When fish migration was perpendicular to the transects, a design in which the survey vessel jumped two transects at a time rather than one resulted in lower biases for migration speeds less than 0.7 m/s (Fig. 9). This was because vessel velocity in the x direction increased when a vessel jumped two transects at a time rather than one only and faster vessel speeds in this direction lowered bias over lower ranges of migration speeds (Fig. 9).

Many acoustic surveys have designs in which transects zigzag systematically across the survey area (Fig. 2, Design 9) (e.g., Dark et al. 1980; Hafsteinsson and Misund 1992). Designs with transects roughly perpendicular to the direction of fish migration had slightly lower biases than ones with parallel transects (Fig. 2, Design 1). This was because survey vessels proceeded faster in the x direction in zigzag designs than in parallel transect designs. Designs with transects parallel to the direction of fish migration had biases slightly higher than those for designs with parallel transects (Fig. 9). This was because vessels proceeded slower in the y direction in zigzag designs than in parallel transect designs.

© 1998 NRC Canada

Fig. 5. % Bias in biomass estimates as a function of the ratio of maximum observable school size to actual school size (r_{max}).

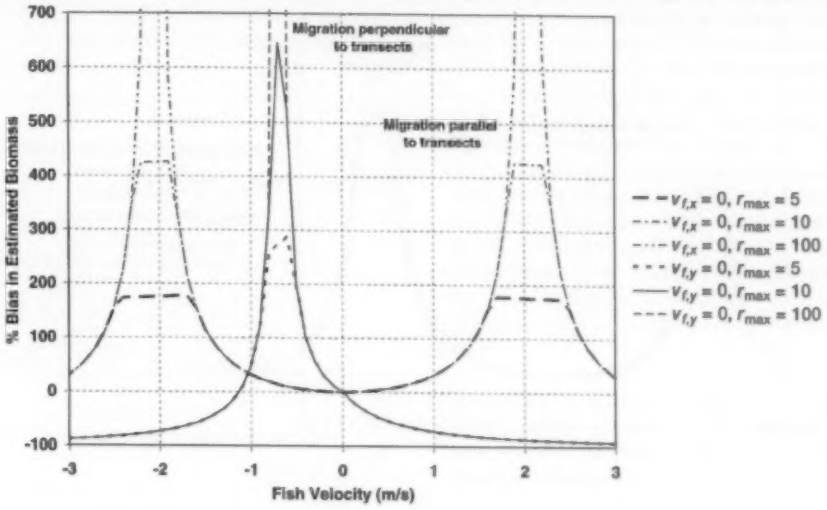
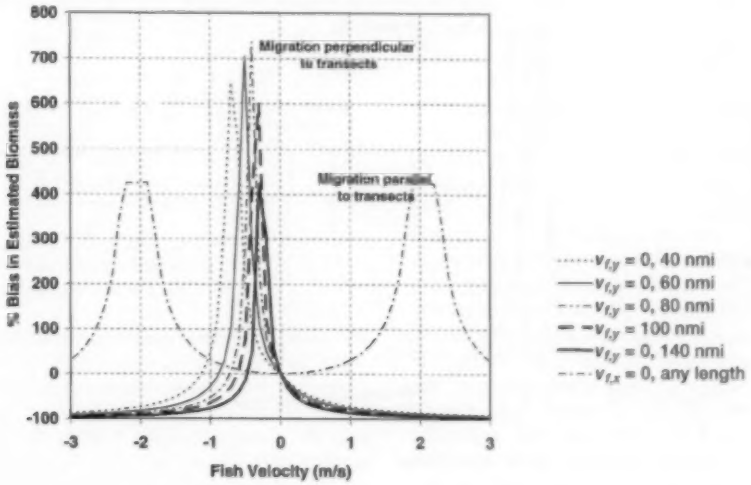

Migration perpendicular to transects
Migration parallel to transects
% Bias in Estimated Biomass
Fish Velocity (m/s)
$v_{f,x} = 0, r_{max} = 5$
$v_{f,x} = 0, r_{max} = 10$
$v_{f,x} = 0, r_{max} = 100$
$v_{f,y} = 0, r_{max} = 5$
$v_{f,y} = 0, r_{max} = 10$
$v_{f,y} = 0, r_{max} = 100$

Fig. 6. % Bias in biomass estimates as a function of the length of each transect.


Migration perpendicular to transects
Migration parallel to transects
% Bias in Estimated Biomass
Fish Velocity (m/s)
$v_{f,y} = 0$, 40 nmi
$v_{f,y} = 0$, 60 nmi
$v_{f,y} = 0$, 80 nmi
$v_{f,y} = 100$ nmi
$v_{f,y} = 0$, 140 nmi
$v_{f,x} = 0$, any length

Interannual variability in estimated biomass

In the first evaluation, the baseline design (Fig. 2, Design 1) was used. For migration velocities less than 1.0 m/s, the CV in biomass estimates, $CV(\hat{B})$, was less than 0.1 for fish vectors in the right-hand quadrants of migration directions (0–0.5 and 1.5–2.0π radians). $CV(\hat{B})$ was least when the direction of migration was aligned parallel to and slightly to the right of the transects (0.3–0.5 and 1.5–1.8π radians), i.e., with the vessel proceeding slightly against the direction of migration as it moved between transects (Fig. 10). $CV(\hat{B})$ could be considerably larger (up to about 0.45) if fish followed the vessel as it moved between transects. Migration speeds higher than 0.75 m/s yielded higher values for $CV(\hat{B})$ over the full range of migration directions.

Increasing the vessel speed (Figs. 11 and 12) reduced the $CV(\hat{B})$, especially when the vessel moved with the direction of migration when it crossed between transects (Fig. 11). Increasing transect length by a factor of, e.g., 2, increased $CV(\hat{B})$ very little when the vessel moved against the direction of migration (Fig. 12). In contrast, $CV(\hat{B})$ increased by up to 700% when the vessel moved in the same direction as the fish.

Designs in which the vessel(s) proceeded only in one direction across the survey area (Fig. 2, Designs 1, 2, 3, and 9) over most conditions had considerably lower $CV(\hat{B})$ than ones in which the vessel(s) proceeded in opposite directions (Designs 4, 5, 6, 7, and 8) (Fig. 13). Designs with two vessels proceeding in the same direction across the survey area (Designs 2 and 3) had lower $CV(\hat{B})$ than similar designs with only one vessel (Design 1). Designs that had two times as many transects in which the vessel(s) proceeded against than with the direction of migration (Designs 2, 4, and 7) had slightly lower $CV(\hat{B})$ than ones with the same number of transects going with as against the direction of migration

© 1998 NRC Canada

Fig. 7. % Bias in biomass estimates as a function of the number of transects.

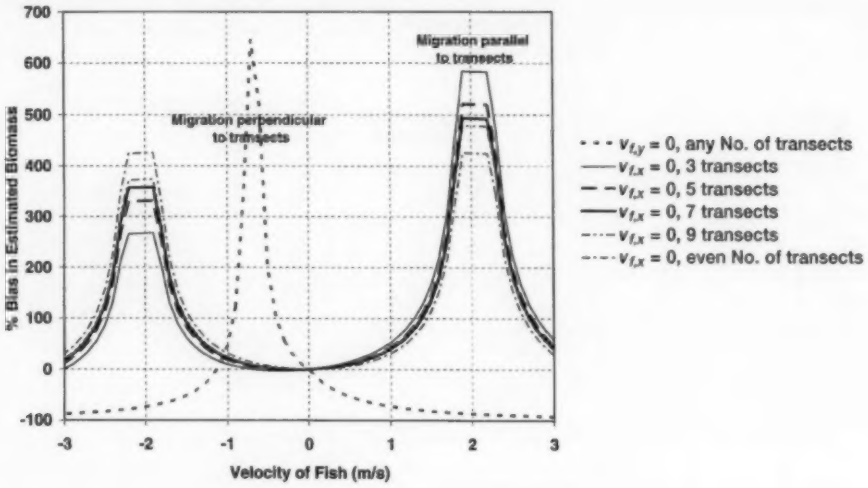

% Bias in Estimated Biomass
Velocity of Fish (m/s)
Migration perpendicular to transects
Migration parallel to transects
$v_{f,y}$ = 0, any No. of transects
$v_{f,x}$ = 0, 3 transects
$v_{f,x}$ = 0, 5 transects
$v_{f,x}$ = 0, 7 transects
$v_{f,x}$ = 0, 9 transects
$v_{f,x}$ = 0, even No. of transects

Fig. 8. % Bias in biomass estimates as a function of the mean vessel speed down the transects ($v_{v,c}$).

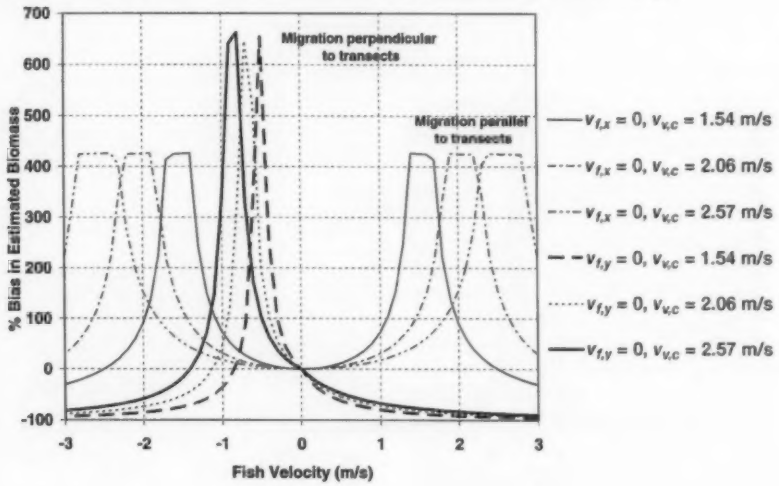

% Bias in Estimated Biomass
Fish Velocity (m/s)
Migration perpendicular to transects
Migration parallel to transects
$v_{f,x}$ = 0, $v_{v,c}$ = 1.54 m/s
$v_{f,x}$ = 0, $v_{v,c}$ = 2.06 m/s
$v_{f,x}$ = 0, $v_{v,c}$ = 2.57 m/s
$v_{f,y}$ = 0, $v_{v,c}$ = 1.54 m/s
$v_{f,y}$ = 0, $v_{v,c}$ = 2.06 m/s
$v_{f,y}$ = 0, $v_{v,c}$ = 2.57 m/s

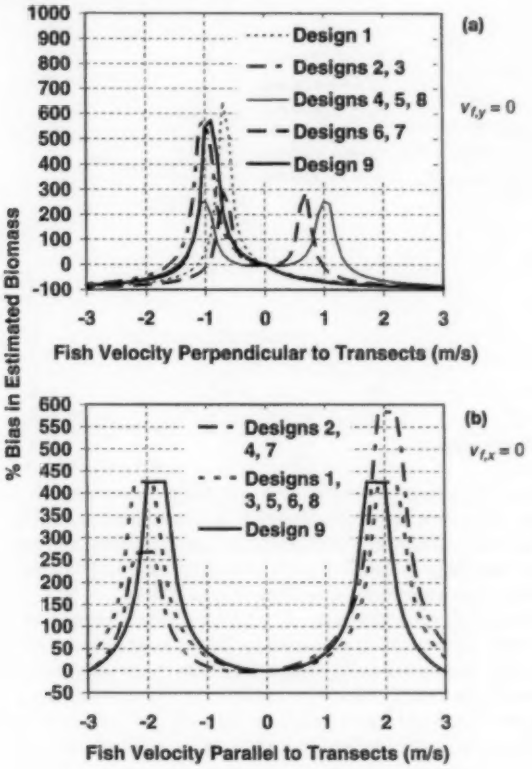
Table 1. Expected values for % bias in acoustic surveys over all directions for some ranges of migration speeds.

	0.0 m/s < v_f < 0.5 m/s			0.5 m/s < v_f < 1.0 m/s			1.0 m/s < v_f < 2.0 m/s		
Design	$E(-)$	$E(+)$	%(+)	$E(-)$	$E(+)$	%(+)	$E(-)$	$E(+)$	%(+)
1	–32	34	55	–49	242	53	–59	246	37
2	–23	17	49	–42	105	53	–55	237	51
3	–26	15	55	–42	103	54	–56	229	52
4	–4	4	33	–5	47	82	–35	139	74
5 and 8	–3	2	20	–1	40	95	–35	137	75
6	–1	172	72	–13	108	99.6	–52	11	47
7	–3	14	64	–3	116	93	–52	172	47
9	–28	18	55	–44	150	54	–56	244	48

Note: The expected values for those biases that are negative, $E(-)$, and those that are positive, $E(+)$, and the percentage of biases that are positive, %(+), are shown.

© 1998 NRC Canada

Fig. 9. % Bias in biomass estimates as a function of the order of execution of survey transects. See Fig. 2 for details on the designs. (*a*) Fish velocity perpendicular to transects; (*b*) fish velocity parallel to transects.



(Designs 3, 5, and 6, respectively). Designs in which vessels jumped two transects at a time (Designs 3 and 5) had lower CV($\hat{B}$) than ones in which the vessel jumped only one at a time (Designs 1 and 6, respectively). The systematic zigzag design (Fig. 2, Design 9) yielded slightly higher CVs than the baseline design (Design 1) for migration directions in the right-hand quadrants and slightly lower ones for those in the left-hand quadrants (Fig. 13). Of the alternatives considered, Design 2 with twice as many transects in which vessel movement was directed against the direction of migration yielded the lowest CVs (Fig. 13).

Discussion

Comparisons with other studies of the effects of migration on abundance estimates

The effects of migration on bias in abundance estimates from research surveys have received some attention but only in relatively few instances (e.g., Hiby 1986; Simmonds 1989; Hafsteinsson and Misund 1992; MacLennan and Simmonds 1992; Simmonds et al. 1992; Buckland et al. 1993). Hiby (1986) evaluated the potential effects on minke whale abundance estimates of different whale movement rates in line transect sighting surveys. Hiby (1986) found that the estimate of sighting rate ratio for different vessel speeds depended critically on random whale movement and could lead to large biases in density estimates if the values used for whale movement were incorrect. Buckland et al. (1993) accounted for the difference in gray whale travel rates between night and day to correct their estimates of abundance that were based on daytime shore-based counts. The estimated correction factor was very close to unity (1.05), however. MacLennan and Simmonds (1992) provided an estimator for bias in acoustic estimates of abundance that indicated that bias could be very large, depending on the movement rates of the vessel and fish. However, as shown above, the estimator has anomalous properties. In contrast, the effects of variability in migration rates on variability in biomass estimates have not been previously evaluated.

Generality of approach and its assumptions

The models presented in this paper for evaluating bias assume that fish migration velocities and directions and vessel velocities along transects are constant during the survey and all fish in a population of interest are within the boundaries of the survey area during its execution. The models would not accurately represent the biases if there were size-dependent, spatial or temporal variation in the velocity components and strong spatial trends in abundance. However, the models could be disaggregated by fish size, or on a transect-by-transect basis or within-transect basis to account for such variability in the velocity components.

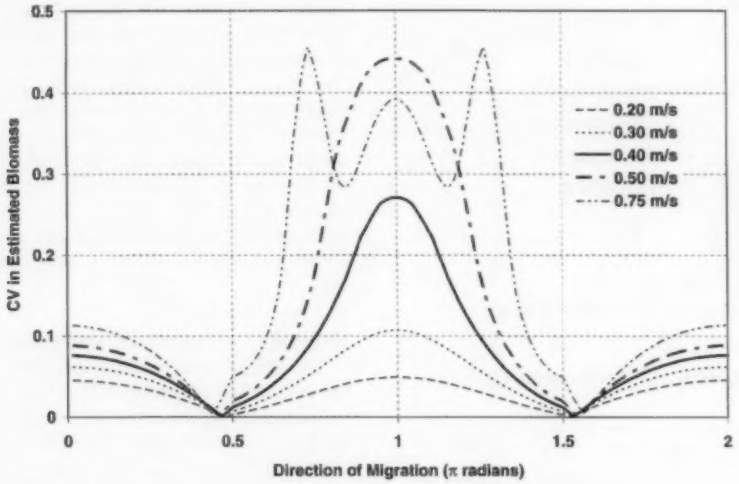
In trawl surveys, it is possible that effects of variability in currents or light, for example, on catchability could be confounded with the effects of migration (Engås and Soldal 1992; Arnold et al. 1994; Michalsen et al. 1996). The main impact of such interactions among these different factors might simply be to increase random error variability in biomass estimates, and the effect of migration on trawl biomass estimates might not be as simple as suggested by eq. 8. These equations still provide a quantitative basis with which to evaluate the implications of migration for trawl surveys and to compare the relative magnitude of the potential effects of the various factors that may bias trawl estimates. Moreover, the main effect of migration on bias in biomass estimates is the distortion caused in the apparent spatial extent of fish aggregations, and this effect will apply to biomass estimates from both trawl and acoustic surveys.

A further assumption is that the horizontal dimensions of fish aggregations are rectangular. This assumption will never be met in nature. However, the model is an approximation and is intended to capture the essential processes that cause bias from migration (i.e., the bias in the estimated area of the fish aggregation that results from fish movement). By incorporating the relative dimensions of the fish aggregation in the x and y directions, and modeling the expected observed distances over the fish in the x and y directions, the model should give a reasonable approximation of the potential directions and magnitudes of the resulting biases in biomass estimates.

The approach in this paper was developed for line transect surveys. In many trawl surveys, however, sampling sites are chosen randomly (often with some constraints). Most of these designs more or less mimic systematic designs in order to minimize traveling time between stations. For example, in

© 1998 NRC Canada

Fig. 10. Monte Carlo estimates of the CV in biomass estimates over the range of possible directions of migrations and at several different migration velocities. The CVs in fish and vessel velocity are set at 0.1. The CV in vessel velocity is set at zero. Results for Design 1 (Fig. 2).



the U.S. west coast groundfish trawl survey, the survey vessel proceeds from south to north along transects that are aligned in an east–west direction and makes hauls at randomly chosen stations along the transects (Dark and Wilkins 1994). In the U.S. east coast trawl survey, sampling stations are chosen randomly in each of several strata and then the most efficient path between the stations is found. This is typically a zigzag-like path from north to the south in the nearshore areas and then northwards in the offshore areas (M. Pennington, Alaska Fisheries Science Center, Seattle, Wash., personal communication).

The results in the analyses above should hold qualitatively for most random types of designs. This is provided that the vessels in random designs progress in one direction across the survey area or in one direction and then in the opposite one. If vessels also take the shortest route through the sampling stations (most often not along straight lines), the rate of vessel movement across a survey area may be faster in random designs (Beardwood et al. 1959). Therefore, the expected biases and variability from migration may be smaller in random designs than in systematic ones.

Implications of migration for bias and variability in biomass estimates and survey design

The largest biases and CVs in biomass estimates occur when fish follow the vessel from transect to transect and, in acoustic surveys, also at the same speed down the transects. Designs that minimized bias and variability from migration had (*i*) vessel speeds considerably greater than fish velocities, (*ii*) the fastest vessel speeds along transects, (*iii*) more vessels, (*iv*) vessels jumping two transects at a time, (*v*) twice as many transects with vessel movement directed against the direction of migration than with, (*vi*) transects aligned parallel to the direction of migration, and (*vii*) the vessel(s) proceeding slightly against the direction of migration as the vessel(s) moves between transects.

Godø (1994) also suggested that the use of more than one vessel in order to quickly survey an area may reduce bias from migration. Variability in catching power among vessels, however, may substantially increase the variability in biomass estimates. Standardization of sampling equipment and sampling protocol at each sampling station could help to lower this source of variability (Godø 1994).

Aligning acoustic transects parallel to the direction of migration so that the biases introduced by migration in the opposing directions will cancel has also been suggested by Simmonds (1989). However, results in the current paper indicate that biases and variances in both acoustic and trawl surveys may yet be smaller if the transects are aligned so that the vessel proceeds at least partially against the direction of migration as it crosses between transects, especially for larger migration speeds (e.g., greater than 0.5 m/s).

The findings in the current paper contrast with recommendations made by MacLennan and Simmonds (1992). They suggested instead that the survey proceed with transects aligned perpendicular to the direction of fish migration and that the vessel proceed in the same direction and then against the direction of migration. Simmonds et al. (1992) suggested that this latter design would reduce variability in biomass estimates if there was a large gradient in fish density that ran perpendicular to the direction of migration. Thereby, the transects would be aligned parallel to the gradient in density, and variability in density among transects would be minimized, and thus also the estimate of biomass. However, interannual variability in biomass estimates can also be increased considerably if the vessel follows the fish across transects (Figs. 10–12). The trade-offs between these alternative sources of bias and variance require careful consideration in the design of surveys in such situations.

Effects of migration in actual surveys

Hafsteinsson and Misund (1992) applied MacLennan and Simmonds' (1992) suggestions for survey design to Icelandic capelin that migrate at a rate of about 0.5 m/s. The average vessel speed was about 1.93 m/s in the same direction as migration and 2.20 m/s in the opposite direction as migra-

© 1998 NRC Canada

Fig. 11. Monte Carlo estimates of the CV in biomass estimates in acoustic surveys when different vessel speeds are considered. The CVs in fish and vessel velocities are set at 0.1. (*a*) Vessel speed 1.54 m/s; (*b*) vessel speed 2.06 m/s; (*c*) vessel speed 2.57 m/s.

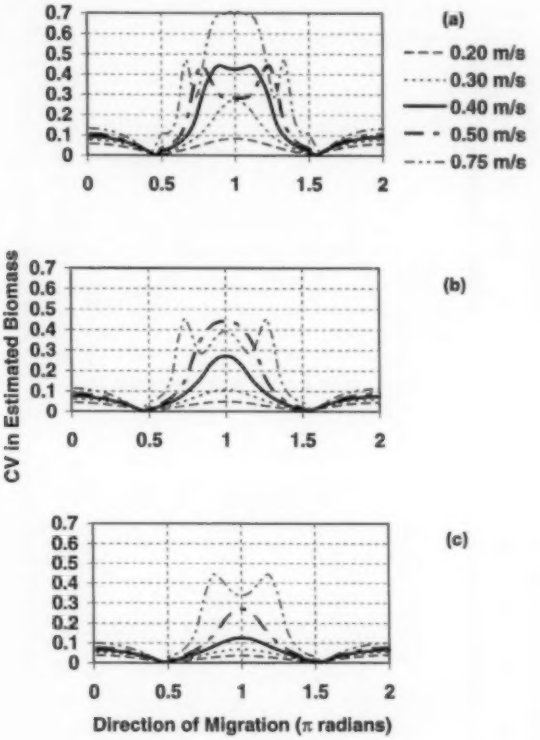
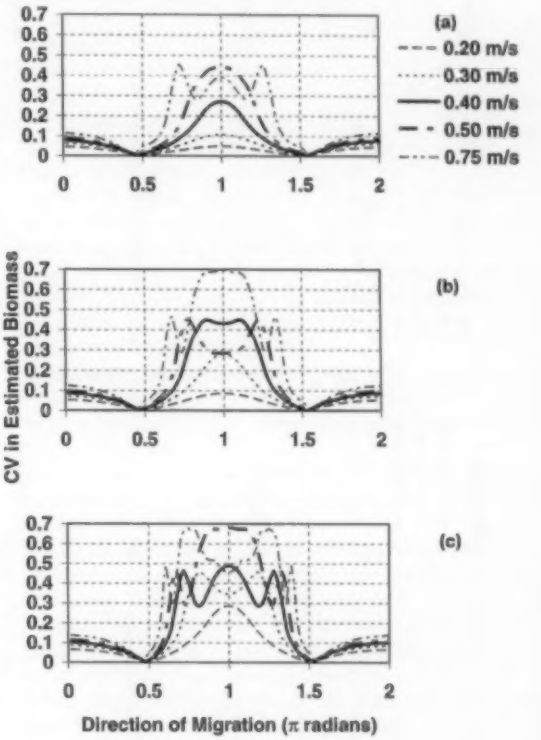


Fig. 12. Monte Carlo estimates of the CV in biomass estimates in acoustic surveys when different transect lengths are considered. The CVs in fish and vessel velocities are set at 0.1. (*a*) 40 nautical miles; (*b*) 60 nautical miles; (*c*) 100 nautical miles.



tion. As expected, the estimate obtained while the vessel was going with the direction of migration (212 000 t) was larger than that going against the direction of migration (126 400 t).

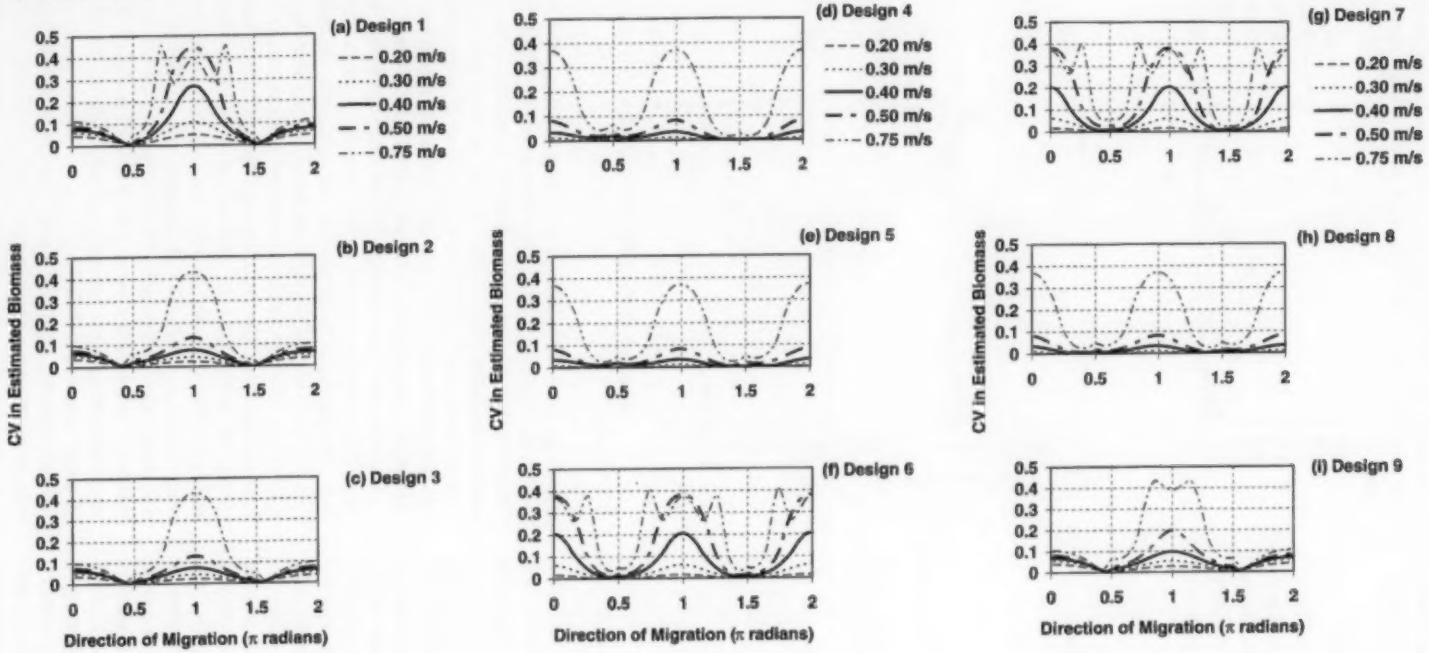
The protocol for the trawl survey in the eastern Bering Sea (Gunderson 1993) also contrasts with the recommendations provided in the current paper. The survey was designed to minimize the impacts on bias in biomass estimates of the northeastward inshore migration of yellowfin sole that takes place during the survey (Wakabayashi 1989). McAllister (1995) suggested an average migration rate of 0.1–0.2 m/s. The migration rate can vary considerably between years depending on the rate that winter ice covers recede (Wilderbuer et al. 1992). The two survey vessels employed follow transects that run in a north–south direction. By proceeding across transects in the direction against migration, biomass estimates will be negatively biased. Using a model presented in this paper (eq. 8), a design with similar specifications to the eastern Bering Sea design resulted in a –30% bias when each of the two vessels averaged 2.52 stations per day (G. Stauffer, RACE Division, National Marine Fisheries Service, Seattle, Wash.) and fish migrated inshore at 0.1 m/s (Fig. 14*a*). With fish migrating at 0.2 m/s, the bias was –50%. In contrast, the biases were negligible when the transects were aligned parallel to the direction of fish migration (Fig. 14*a*). However, in the current design, the CV introduced in biomass estimates was less than the CVs for interannual variation in migration velocities and vessel speeds combined (Fig. 14*b*). This is not so for a design in which transects are parallel to migration. Therefore the design currently used in the eastern Bering Sea may present a reasonable compromise between variance and bias.

Variations in the execution of trawl surveys in the eastern Bering Sea corroborate the large biases in biomass estimates that can result from migration. For example, in August–October 1975 the survey was conducted after the inshore migration. In 1976, however, the survey was conducted April–June and followed the receding ice edge and the inshore migration of yellowfin sole (Bakkala and Smith 1978). Estimates of yellowfin sole biomass were twice as high in 1976 as in 1975, i.e., 2 094 600 t compared with 1 038 600 t. This difference, the largest interannual difference in estimates of yellowfin sole biomass ever, was attributed partly to the survey following the inshore migration in 1976 but not in 1975 (Bakkala and Smith 1978).

The sampling error CV for the estimate in 1976 (0.23) was also far larger than that in 1975 (0.08) or any since (e.g., 0.09 in 1988, data obtained from G. Walters, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, Wash.). The high CV was obtained even though the

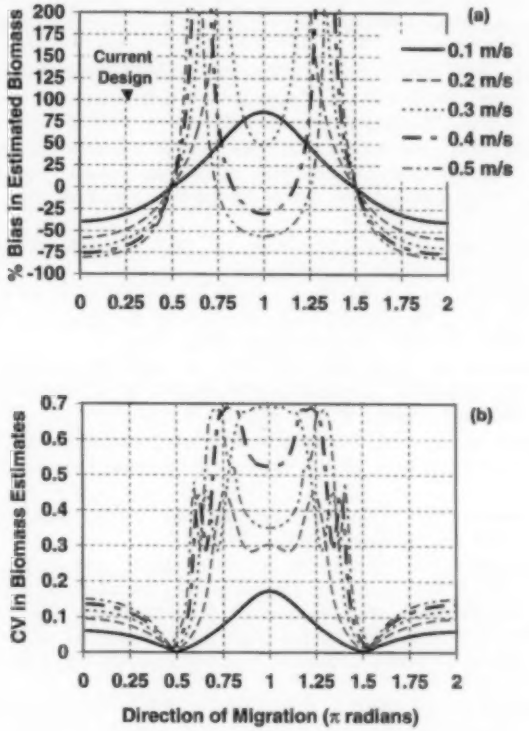
© 1998 NRC Canada

Fig. 13. Monte Carlo estimates of the CV in biomass estimates in acoustic surveys when different protocols for traversing transects are considered. The CVs in fish and vessel velocities are set at 0.1.



© 1998 NRC Canada

Fig. 14. (*a*) % Bias in trawl survey estimates of biomass for a survey design similar to that used in the eastern Bering Sea. (*b*) CVs in biomass estimates assuming that the CVs in fish and vessel velocity are 0.1. The design had an average of 10 stations per transect and 20 transects, and the two vessels moved at a rate of 2.5 stations per day. Towing speed was 1.54 m/s. Design 2 in Fig. 2 depicts the protocol for vessel movement across the design.



number of stations sampled was very large (435) compared with that used other years (e.g., about 350 since 1981). It has already been shown that small interannual variability in fish and vessel velocities can cause large error variability in biomass estimates, especially if the vessel follows the fish as it crosses transects. A high within-year sampling error CV may also be expected in such situations because the distances across and between fish aggregations will be enlarged when a survey vessel follows the fish. Thus, the interaction of fish migration and survey protocol may have been the major source of sampling error variability in the 1976 estimate (Bakkala and Smith 1978).

In this paper, bias in biomass estimates in acoustic and trawl surveys was modeled as a function of fish and vessel velocity vectors on a transect-by-transect basis. The models can be used to estimate the biases and variability from migration in historic biomass estimates. They can also be used to redesign existing surveys or design new surveys by helping to find a reasonable compromise between bias and variance in estimates of abundance. The models only apply providing that fish remain within the survey area during the survey.

The major conclusions are as follows.

(1) Fish migration during acoustic and trawl surveys of fish abundance can distort the observed area across fish aggregations and increase the bias and variance in estimates of fish density and biomass.
(2) Even relatively low migration velocities (e.g., 0.3 m/s) can cause large biases (e.g., >200%) in acoustic and trawl survey biomass estimates.
(3) If there is migration in the x direction (i.e., perpendicular to the transects), the ratio of the y to the x dimensions of the overall fish aggregation in the survey area can be important in determining the total direction and magnitude of bias in biomass estimates. Increases in the ratio of the y to the x dimensions of a fish aggregation will cause decreases in biomass estimates.
(4) Bias can potentially be larger in acoustic surveys because in trawl surveys the bias in density estimates from individual hauls may counteract the bias in density estimates across transects.
(5) Relatively small interannual variability in migration rates and vessel velocity (e.g., CV = 0.1) can cause large interannual error variability in biomass estimates (e.g., CV > 0.4).
(6) The amount of bias and variability introduced by migration depends strongly on the direction and speed of migration and survey design.
(7) The most important aspect of survey design with regard to variability and bias from migration is the alignment of survey transects with respect to the direction of migration. In both acoustic and trawl surveys, the alignment that tends to minimize bias and variance for the most common migration speeds (v_f < 1.0 m/s, Harden Jones 1968) is one in which the transects are roughly parallel to the direction of migration and the vessel proceeds slightly against the direction as it moves between transects. In contrast, very large bias and variance in biomass estimates can result if the vessel proceeds in the same direction as migration as it crosses between transects.
(8) Designs suggested by others (e.g., MacLennan and Simmonds 1992) in which the survey vessel first proceeds with and then against the direction of fish migration as it proceeds across transects can cause large positive bias and interannual error variability in biomass estimates at least for fish velocities greater than 0.6 m/s.
(9) Longer transects will tend to increase the magnitude of bias and error variance from migration, especially if migration goes perpendicular to the transects.
(10) The number of transects in a survey is not that important with respect to bias and error variability in biomass estimates.
(11) Slower cruising speeds will tend to increase the magnitude of the bias and error variability in biomass estimates.

The models for bias require estimates of fish and vessel velocity vectors. Vessel velocity vectors can be accurately estimated using geographic positioning systems or loran. Fish velocity vectors are considerably more difficult to estimate. These can be estimated from mark and recapture experiments (e.g., Godø 1989; Wakabayashi 1989), radiotagging (Buckland et al. 1993), or tracking fish aggre-

© 1998 NRC Canada

gations using sonar (Hafsteinsson and Misund 1992). Any one of these can be used to assess the best surveying strategy on average (Godø 1994). The latter two approaches can also be used to adapt an ongoing survey to the current state of migration (e.g., to ensure that the survey encompasses the spatial extent of the fish population in each year (Godø 1989)). Because of the potentially large biases and variances from migration in surveys of abundance, studies to estimate fish migration vectors may be well worth their costs. However, the best advice, should it be possible, is to conduct surveys when fish are not migrating.

Acknowledgments

I thank Don Gunderson, Ellen Pikitch, Gary Stauffer, Judy Zeh, Andre Punt, Julie Rousseau, Luis Borda de Agua, Geoff Kirkwood, and Ray Hilborn for helpful suggestions. Thanks also go to Gary Walters, Michael Pennington, Mark Wilkins, Peter Monroe, and Craig Rose for helpful discussions. Alav Rune Godø is thanked for his helpful comments on an earlier version of this paper. The work was funded by a grant from the U.S. National Marine Fisheries Service.

References

Aglen, A. 1994. Sources of error in acoustic estimates of fish abundance. *In* Marine fish behaviour and abundance estimation. *Edited by* A. Fernö and S. Olsen. Fishing News Books, Cambridge, Mass: pp. 107–133.

Arnold, G.P., Greer Walker, M., Emerson, L.S., and Holford, B.H. 1994. Movements of cod (*Gadus morhua*) in relation to the tidal streams in the southern North Sea. ICES J. Mar. Sci. **51**: 207–232.

Bakkala, R.G., and Smith, G.B. 1978. Demersal fish resources of the eastern Bering Sea: spring 1976. Processed Rep., Northwest and Alaska Fisheries Center, Seattle.

Beardwood, J., Halton, J.H., and Hammersley, J.M. 1959. The shortest path through many points. Proc. Cambridge Philos. Soc. **55**: 299–327.

Buckland, S.T., Breiwick, J.M., Cattanach, K.L., and Laake, J.L. 1993. Estimated population size of the California gray whale. Mar. Mammal Sci. **9**: 235–249.

Byrne, C.J., Azarovitz, T.R., and Sissenwine, M.P. 1981. Factors affecting variability of research vessel trawl surveys. *In* Bottom trawl surveys. *Edited by* W.G. Doubleday and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 58. pp. 258–273.

Dark, T.A., and Wilkins, M.E. 1994. Distribution, abundance, and biological characteristics of groundfish off the coast of Washington, Oregon, and California, 1977–1986. U.S. Dep. Commer. NOAA Tech. Rep. NMFS 117.

Dark, T.A., Nelson, M.O., Traynor, J.J., and Nunallee, E.P. 1980. The distribution, abundance and biological characteristics of Pacific hake, *Merluccius productus*, in the California – British Columbia region during July–September, 1977. Mar. Fish. Rev. **42**(3–4): 17–33.

Engås, A., and Soldal, A.V. 1992. Diurnal variations in bottom trawl catch rates of cod and haddock and their influence on abundance indices. ICES J. Mar. Sci. **49**: 89–95.

Godø, O.R. 1989. The use of tagging studies to determine the optimal time for estimating acoustic abundance. Fish. Res. **8**: 129–140.

Godø, O.R. 1994. Factors affecting the reliability of groundfish abundance estimates from trawl surveys. *In* Marine fish behaviour and abundance estimation. *Edited by* A. Fernö and S. Olsen. Fishing News Books, Cambridge, Mass. pp. 166–199.

Gunderson, D.R. 1993. Surveys of fisheries resources. John Wiley & Sons Inc., New York.

Hafsteinsson, M.T., and Misund, O.A. 1992. The possible influence of migration speed on acoustic assessment of capelin (*Mallotus villosus*) (Muller 1776) at Iceland. Fisheries Technology and Fish Behaviour Working Group. International Council for the Exploration of the Sea. Copenhagen, Denmark.

Harden-Jones, F.R. 1968. Fish migration. Edward-Arnold, London, U.K.

Hiby, A.R. 1986. Results of a hazard rate model relevant to experiments on the 1984/85 IDCR minke whale assessment cruise. Rep. Int. Whaling Comm. **36**: 497–499.

Karp, W.A., and Walters, G.E. 1994. Survey assessment of semipelagic gadoids: the example of walleye pollock, *Theragra chalcogramma*, in the eastern Bering Sea. Mar. Fish. Rev. **56**: 8–22.

MacLennan, D.N., and Simmonds, J.E. 1992. Fisheries acoustics. Chapman and Hall, London, U.K.

McAllister, M.K. 1995. Using decision analysis to choose a design for surveying fisheries resources. Ph.D. thesis, School of Fisheries, University of Washington, Seattle, Wash.

Michalsen, K., Godø, O.R., and Ferno, A. 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indices. ICES J. Mar. Sci. **53**: 389–395.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. Charles Griffin and Company Ltd., London, U.K.

Simmonds, E.J. 1989. Survey and data analysis procedures. ICES FAST Working Group, Dublin, Ireland.

Simmonds, E.J., Williamson, N.J., Gerlotto, F., and Aglen, A. 1992. Acoustic survey design and analysis procedure: a comprehensive review of current practice. ICES Coop. Res. Rep. 187.

Wakabayashi, K. 1989. Studies on the fishery biology of yellowfin sole in the eastern Bering Sea. Bull. Far Seas Fish. Res. Lab. **26**: 21–152.

Wilderbuer, T.K., Walters, G.E., and Bakala, R.G. 1992. Yellowfin sole, *Pleuronectes asper*, of the eastern Bering Sea: biological characteristics, history of exploitation, and management. Mar. Fish. Rev. **54**: 1–18.

Appendix. Derivation of bias from migration in acoustic estimates of biomass

The material in this appendix was extracted from McAllister (1995, appendix E). In order to evaluate the bias in the estiimated density on each survey transect, $\hat{D}_t$, that results from the movement of fish and the survey vessel, we need an expression for the expected value for $\hat{D}_t$, $E(\hat{D}_t)$, the mean value of $\hat{D}_t$ across all potential spatial arrays of the fish aggregations in the survey area. $E(\hat{D}_t)$ can be expressed as the conditional expectation

$$(1.1) \quad E(\hat{D}_t) = E(\hat{D}_t | \hat{D}_t \neq 0) P(\hat{D}_t \neq 0)$$

where $E(\hat{D}_t | \hat{D}_t \neq 0)$ is the expected value for $\hat{D}_t$ given that $\hat{D}_t$ in transect t is nonzero and $P(\hat{D}_t \neq 0)$ is the probability that $\hat{D}_t$ in transect t is nonzero.

We will first develop an expression for $E(\hat{D}_t | \hat{D}_t \neq 0)$. This quantity can be expressed by

© 1998 NRC Canada

$$(1.2)\quad E(\hat{D}_l \mid \hat{D}_l \neq 0) = E\left(D_f \frac{d_y^{obs}}{L_t}\right) = \frac{D_f}{L_t} E(d_y^{obs})$$

where D_f is the true mean density of the fish within aggregations, d_y^{obs} is the distance along the transect in which fish are observed given that fish are observed on this transect, and L_t is the length of the transect. d_y^{obs} is considered to be a random variable that varies depending on the point along the x-axis that the vessel encounters the fish aggregation.

The expected observed distance of the fish aggregation along the y-axis, $E(d_y^{obs})$, can be expressed by

$$(1.3)\quad E(d_y^{obs}) = E\left(|v_{v,y}|\, t(d_y^f)\right) = |v_{v,y}|\, E(t(d_y^f))$$

where $v_{v,y}$ is the velocity vector of the vessel in the y direction and $t(d_y^f)$ is the time that it takes for the vessel to traverse the distance d_y^f, the distance across the fish on the y-axis. The absolute value of $v_{v,y}$ is taken in eq. 1.3 (and for other velocity vectors in equations below) because distance and time are nonnegative quantities and the absolute value of velocity has to be taken in order for distance and time to remain nonnegative. The expected time that it takes for the vessel to travel across the fish in the y direction is the expectation of the distance across the fish divided by the relative velocity of the vessel across the fish:

$$(1.4a)\quad E(t(d_y^f)) = E\left(\frac{d_y^{trav}}{|v_{v,rel(f),y}|}\right) = \frac{E(d_y^{trav})}{|v_{v,y} - v_{f,y}|}$$

where d_y^{trav} is the distance across the fish that is traversed by the vessel, $v_{v,rel(f),y}$ is the relative velocity of the vessel over the fish, and $v_{f,y}$ is the velocity vector of the fish in the y direction. $v_{v,rel(f),y}$ is positive if the vessel is moving up the y-axis and against the fish or faster than the fish and in the same direction. However, $v_{v,rel(f),y}$ will be negative if the fish are moving up the y-axis at a rate faster than the vessel. In this latter case the expression still gives the time that it takes for the fish to pass beneath the vessel.

If fish were moving only in the y direction (i.e., $v_{f,x} = 0$), then

$$(1.4b)\quad E(d_y^{trav}) = \bar{d}_y^f$$

and

$$(1.4c)\quad E(t(d_y^f)) = \frac{\bar{d}_y^f}{|v_{v,y} - v_{f,y}|}$$

where $\bar{d}_y^f$ is the mean height of the fish aggregation on the y-axis (see Fig. 1). Using eqs. 1.3, 1.4a, and 1.4c:

$$(1.5a)\quad E(d_y^{obs}) = \frac{|v_{v,y}|\bar{d}_y^f}{|v_{v,y} - v_{f,y}|}.$$

It should be noted that d_y^{obs} by definition can be no longer than the length, L, of a transect. Thus:

$$(1.5b)\quad E(d_y^{obs}) \leq L, \frac{|v_{v,y}|\bar{d}_y^f}{|v_{v,y} - v_{f,y}|} \leq L, \text{ and } \frac{|v_{v,y}|}{|v_{v,y} - v_{f,y}|} \leq \frac{L}{\bar{d}_y^f}.$$

These three inequalities are a formal statement of the assumption that fish remain confined within the survey area during the survey.

However, if $v_{f,x} \neq 0$, then the expected distance traversed over the fish, $E(d_y^{trav})$, is not necessarily equal to the mean distance across the fish $\bar{d}_y^f$ in the y direction and eq. 1.5a may not hold. For example, if fish were moving to the left and the vessel encountered the aggregation near to its right-hand side, the vessel would traverse the lower right-hand corner of the aggregation and could exit the trailing right-hand edge of the fish (see transect 3 in Fig. A1); the vessel would traverse less than the distance $\bar{d}_y^f$ across the fish in the y direction. Thus, if $v_{f,x} \neq 0$:

$$(1.6)\quad E(d_y^{trav}) \leq \bar{d}_y^f, E(t(d_y^{trav})) \leq t(\bar{d}_y^f), \text{ and } E(d_y^{obs}) \leq |v_{v,y}|t(\bar{d}_y^f).$$

An expression for $E(d_y^{obs})$ given that $v_{f,x} \neq 0$ can be obtained by finding expressions for the expected distance traversed over the fish across all potential points of encounter of the fish aggregation, $E(d_y^{trav})$, and the expected time that it takes to traverse encountered fish aggregations along the y-axis, $E(t(d_y^{trav}))$. Take, for example, the case where $|v_{f,x}|t(\bar{d}_y^f) < \bar{d}_y^f$ where $v_{f,x}$ is the velocity vector of the fish in the x direction. In this case, the vessel would exit the top side of the fish aggregation for at least some of the entry points on the base of the fish aggregation (e.g., transect 2 in Fig. A1). For the simple case in which the fish aggregation is rectangular, $E(d_y^{trav})$ can be expressed as the weighted mean of $E(d_y^{trav})$ when the distance $\bar{d}_y^f$ over the fish in the y direction is traversed, $E(d_y^{trav} \mid d_y^{trav} = \bar{d}_y^f)$, and $E(d_y^{trav} \mid d_y^{trav} < \bar{d}_y^f)$ when less than the distance $\bar{d}_y^f$ is traversed. The weights would be the distances in the x direction in which the two expectations are taken. The first of the two expectations will be $\bar{d}_y^f$ for some fraction of distance along the x-axis in which the aggregation can be encountered (see transect 2 in Fig. A1). The second expectation would be the mean of d_y^{trav} over the other fraction of the distance along the x-axis, $E(d_y^{trav} \mid d_y^{trav} < \bar{d}_y^f)$ (see transects 1 and 3 in Fig. A1). If the fish school is rectangular, and velocities of fish and vessel are constant, then d_y^{trav} will be a linear function of distance in the x direction between the x coordinates that correspond to $d_y^{trav} = \bar{d}_y^f$ and $d_y^{trav} = 0$ (Fig. A1), i.e. $x(d_y^{trav} = \bar{d}_y^f)$ and $x(d_y^{trav} = 0)$, respectively. This implies that the mean value of d_y^{trav} over this segment will be equal to $0.5\bar{d}_y^f$. For example, if $a = \bar{d}_y^f$ and $b = x(d_y^{trav} = \bar{d}_y^f) - x(d_y^{trav} = 0)$ and y as a function of x is described by the linear function $y = (a/b)x$, then:

$$(1.7a)\quad E(y \mid 0 < x < b) = \frac{1}{b}\int_{x=0}^{x=b} \frac{a}{b} x\,dx = \frac{ax^2}{2b^2}\Bigg|_{x=0}^{x=b} = \frac{a}{2} = 0.5\bar{d}_y^f.$$

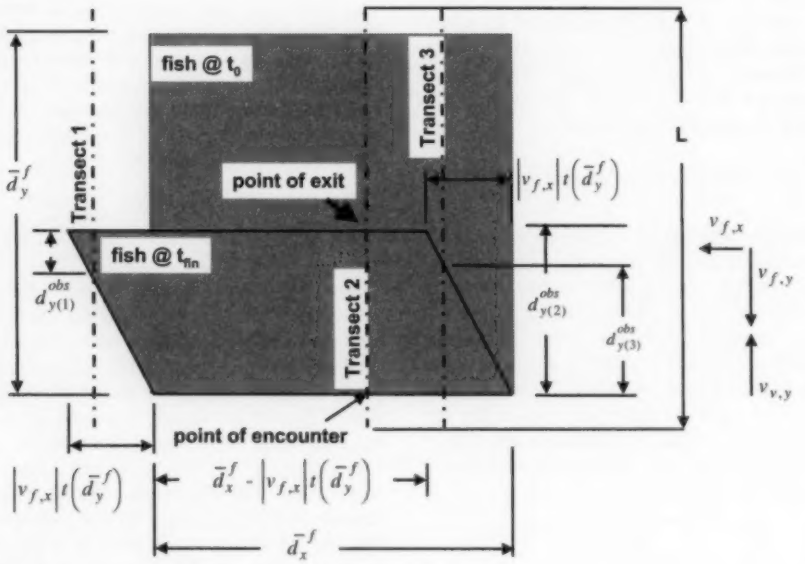
Thus:

$$(1.7b)\quad E(d_y^{trav} \mid 0 < d_y^{trav} < \bar{d}_y^f) = 0.5\bar{d}_y^f.$$

The distance in the x direction in which the condition $0 < d_y^{trav} < \bar{d}_y^f$ holds will be determined by the distance that the fish move in the x direction as the vessel traverses the full extent of the fish in the y direction. For example, if the ves-

© 1998 NRC Canada

Fig. A1. Schematic diagram of the dimensions of a fish aggregation as they would appear to a vessel moving along a transect when the velocity of fish in the x and y directions is negative and the velocity of the vessel in the y direction is positive. The relative velocity of the vessel across the fish in the y direction is greater than the velocity of fish in the x direction. Fish @ t_0 refers to the position of the fish when the vessel first encounters the fish; fish @ t_{fin} refers to the position of the fish when the vessel exits the aggregation. $d^{obs}_{y(1)}$, $d^{obs}_{y(2)}$, and $d^{obs}_{y(3)}$ refer to the observed distances in the y direction across the fish in transects 1, 2, and 3. See Appendix for explanation.



sel starts at the lower left-hand corner of the fish aggregation and the fish aggregation is moving to the left, the trailing edge of the fish will move the distance $|v_{f,x}|t(\bar{d}^f_y)$ in the x direction before the vessel reaches the top side of the aggregation (Fig. A1). If the vessel encounters the fish at less than the distance $|v_{f,x}|t(\bar{d}^f_y)$ from the right-hand edge of the fish, it will exit the trailing edge and will traverse a distance over the fish in the y direction less than $\bar{d}^f_y$ (e.g., transect 3 in Fig. A1). Therefore, $|v_{f,x}|t(\bar{d}^f_y)$ represents the distance in the x direction on the right-hand side of the aggregation that $0 < d^{trav}_y < \bar{d}^f_y$ (Fig. A1). $|v_{f,x}|t(\bar{d}^f_y)$ also represents the distance to the left of the aggregation in which the vessel can encounter the leading edge of the fish as it moves to the left and traverse a distance over the fish less than $\bar{d}^f_y$ (e.g., transect 1 in Fig. A1). Therefore the distance in which $0 < d^{trav}_y < \bar{d}^f_y$ is given by $2|v_{f,x}|t(\bar{d}^f_y)$. The distance on the x-axis in which $d^{trav}_y = \bar{d}^f_y$ is given by the distance along the base of the fish aggregation less the distance in this segment in which $0 < d^{trav}_y < \bar{d}^f_y$: $\bar{d}^f_y - |v_{f,x}|t(\bar{d}^f_y)$ (see transect 2 in Fig. A1). The weighted mean for $E(d^{trav}_y)$ can thus be expressed by

$$(1.8a)\quad E(d^{trav}_y) = \frac{2|v_{f,x}|t(\bar{d}^f_y)}{\bar{d}^f_x + |v_{f,x}|t(\bar{d}^f_y)}(0.5\bar{d}^f_y) + \frac{\bar{d}^f_x - |v_{f,x}|t(\bar{d}^f_y)}{\bar{d}^f_x + |v_{f,x}|t(\bar{d}^f_y)}(\bar{d}^f_y).$$

This equation can be simplified as follows:

$$(1.8b)\quad E(d^{trav}_y) = \frac{\left\{|v_{f,x}|t(\bar{d}^f_y) + \bar{d}^f_x - |v_{f,x}|t(\bar{d}^f_y)\right\}\bar{d}^f_y}{\bar{d}^f_x + |v_{f,x}|t(\bar{d}^f_y)}$$

$$(1.8c)\quad E(d^{trav}_y) = \frac{\bar{d}^f_x\bar{d}^f_y}{\bar{d}^f_x + |v_{f,x}|t(\bar{d}^f_y)}.$$

Using eq. 1.4*c*:

$$(1.8d)\quad E(d^{trav}_y) = \frac{\bar{d}^f_x\bar{d}^f_y}{\bar{d}^f_x + |v_{f,x}|\left(\dfrac{\bar{d}^f_y}{|v_{v,y} - v_{f,y}|}\right)}$$

$$(1.8e)\quad E(d^{trav}_y) = \frac{\bar{d}^f_x\bar{d}^f_y|v_{v,y} - v_{f,y}|}{\bar{d}^f_x|v_{v,y} - v_{f,y}| + |v_{f,x}|\bar{d}^f_y}$$

$$(1.8f)\quad E(d^{trav}_y) = \frac{\bar{d}^f_y|v_{v,y} - v_{f,y}|}{|v_{v,y} - v_{f,y}| + |v_{f,x}|\dfrac{\bar{d}^f_y}{\bar{d}^f_x}}.$$

Notice that if

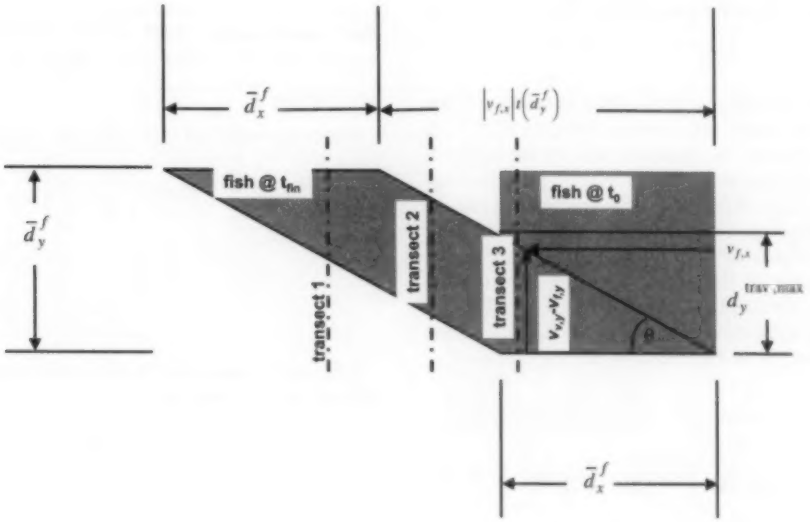
$$(1.8g)\quad \bar{d}^f_x \cong \bar{d}^f_y$$

then

$$(1.8h)\quad E(d^{trav}_y) \cong \frac{\bar{d}^f_y|v_{v,y} - v_{f,y}|}{|v_{v,y} - v_{f,y}| + |v_{f,x}|}.$$

© 1998 NRC Canada

Fig. A2. Schematic diagram of the shape of a fish aggregation as it would appear to a survey vessel if the velocity of the fish in the x direction was greater than the relative velocity of the vessel over the fish. Fish @ t_0 refers to the position of the fish when the vessel first encounters the fish; fish @ t_{fin} refers to the position of the fish when the vessel exits the aggregation. See Appendix for an explanation.



Now, recalling eqs. 1.3 and 1.4*a*,

$$(1.8i)\quad E(d_y^{obs}) = |v_{v,y}|E[t(d_y^{trav})]$$

$$(1.8j)\quad E[t(d_y^{trav})] = E\left[\frac{d_y^{trav}}{|v_{v,y} - v_{f,y}|}\right] = \frac{E(d_y^{trav})}{|v_{v,y} - v_{f,y}|}.$$

Thus:

$$(1.8k)\quad E(d_y^{obs}) = E\frac{|v_{v,y}|}{|v_{v,y} - v_{f,y}|}E(d_y^{trav,f}) = \frac{|v_{v,y}|}{|v_{v,y} - v_{f,y}|}\cdot\frac{\bar{d}_y^f|v_{v,y} - v_{f,y}|}{|v_{v,y} - v_{f,y}| + |v_{f,x}|\frac{\bar{d}_y^f}{\bar{d}_x^f}}$$

$$(1.8l)\quad E(d_y^{obs}) = \frac{\bar{d}_y^f|v_{v,y}|}{|v_{v,y} - v_{f,y}| + |v_{f,x}|\frac{\bar{d}_y^f}{\bar{d}_x^f}}.$$

It should be noted that the observable distance of fish in the y direction can be no longer than the length of a transect, L. Thus:

$$(1.8m)\quad d_y^{obs} \le L,\ \frac{|v_{v,y}|\bar{d}_y^f}{|v_{v,y} - v_{f,y}| + |v_{f,x}|\frac{\bar{d}_y^f}{\bar{d}_x^f}} \le L, \text{ and } \frac{|v_{v,y}|}{|v_{v,y} - v_{f,y}| + |v_{f,x}|\frac{\bar{d}_y^f}{\bar{d}_x^f}} \le \frac{L}{\bar{d}_y^f}.$$

This latter result will be used below.

The expression for $E(d_y^{obs})$ was developed under the condition that $|v_{f,x}|t(\bar{d}_y^f) < \bar{d}_y^f$. For the case where $|v_{f,x}|t(\bar{d}_y^f) \ge \bar{d}_y^f$, the expression remains the same. This is shown as follows. If $|v_{f,x}|t(\bar{d}_y^f) \ge \bar{d}_y^f$, the distance $\bar{d}_y^f$ is never fully traversed (see Fig. A2). After meeting the fish at any point on the base of the aggregation, the vessel will exit the trailing edge of the fish on the x-axis before the vessel reaches the top side of the aggregation (e.g., transect 3 in Fig. A2). The maximum distance in the y direction that can be traversed, $d_y^{trav,max}$, is the y coordinate of the path across the fish that the vessel sweeps from the leading to the trailing edge of the fish (e.g., transect 2 in Fig. A2). $d_y^{trav,max}$ can be expressed by using the angle θ between the base of the aggregation and the trailing edge of the aggregation as the trailing edge would appear to the vessel over all potential points of encounter along the base of the aggregation (Fig. A2). The tangent of θ can be obtained by dividing the distance traveled by the vessel across the fish in the y direction by the distance traveled by the fish in the x direction before the vessel exits the trailing edge of the fish:

$$(1.9a)\quad \tan\theta = \frac{|v_{v,rel(f),y}|t(d_y^{trav}|d_y^{trav} < d_y^{trav,max})}{|v_{f,x}|t(d_y^{trav}|d_y^{trav} < d_y^{trav,max})} = \frac{|v_{v,y} - v_{f,y}|}{|v_{f,x}|}$$

where $t(d_y^{trav}|d_y^{trav} < d_y^{trav,max})$ is the time that it takes to traverse the fish in the y direction given that the distance traversed across the fish in the y direction is less than $d_y^{trav,max}$. $\tan\theta$ is also given by (see Fig. A2)

$$(1.9b)\quad \tan\theta = \frac{d_y^{trav,max}}{\bar{d}_x^f}.$$

Thus, by eqs. 1.9*a* and 1.9*b*,

© 1998 NRC Canada

$$(1.9c)\quad d_y^{\text{trav,max}} = \frac{\bar{d}_x^{\text{f}}\left|v_{\text{v},y} - v_{\text{f},y}\right|}{\left|v_{\text{f},x}\right|}.$$

Analogously to eq. 1.7*a* when $\left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) < \bar{d}_y^{\text{f}}$:

$$(1.10)\quad E(d_y^{\text{trav}} \mid 0 < d_y^{\text{trav}} < d_y^{\text{trav,max}}) = 0.5 d_y^{\text{trav,max}}.$$

The distance in the x direction over which this expectation holds is $2\bar{d}_x^{\text{f}}$, i.e., the vessel will traverse less than $d_y^{\text{trav,max}}$ if it enters the base or exits the opposite side of the aggregation and these two distances are nonoverlapping on the segment of the x-axis over which the fish aggregation can be encountered (see transects 1 and 3 in Fig. A2). The distance on the x-axis over which $d_y^{\text{trav,max}}$ holds is given by the distance (as would appear to the vessel) in the x direction between, for example, the left-hand side of the base of the fish aggregation and the right-hand side of the top of the fish aggregation (see transect 2 in Fig. A2): $\left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) - \bar{d}_x^{\text{f}}$.

$$E\left(d_y^{\text{trav}} \middle| \left|v_{\text{f},x}\right| \geq \left|v_{\text{v,rel(f)},y}\right|\right)$$

where $v_{\text{v,rel(f)},y} = v_{\text{v},y} - v_{\text{f},y}$, can be obtained from the weighted mean:

$$(1.11a)\quad E\left(d_y^{\text{trav}} \middle| \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) \geq \bar{d}_y^{\text{f}}\right) = \frac{2\bar{d}_x^{\text{f}}}{\bar{d}_x^{\text{f}} + \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}})} \times [0.5 d_y^{\text{trav,max}}] + \frac{\left(\left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) - \bar{d}_x^{\text{f}}\right)}{\bar{d}_x^{\text{f}} + \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}})} [d_y^{\text{trav,max}}]$$

This expression can be simplified as follows:

$$(1.11b)\quad E\left(d_y^{\text{trav}} \middle| \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) \geq \bar{d}_y^{\text{f}}\right) = \frac{\left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}})\, d_y^{\text{trav,max}}}{\bar{d}_x^{\text{f}} + \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}})}$$

$$(1.11c)\quad E\left(d_y^{\text{trav}} \middle| \left|v_{\text{f},x}\right| \geq \left|v_{\text{v},y} - v_{\text{f},y}\right|\right) = \frac{\left|v_{\text{f},x}\right| d_y^{\text{trav,max}}}{\frac{\bar{d}_x^{\text{f}}}{t(\bar{d}_y^{\text{f}})} + \left|v_{\text{f},x}\right|}$$

$$(1.11d)\quad E\left(d_y^{\text{trav}} \middle| \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) \geq \bar{d}_y^{\text{f}}\right) = \frac{\left|v_{\text{f},x}\right| d_y^{\text{trav,max}}}{\frac{\bar{d}_x^{\text{f}}}{\bar{d}_y^{\text{f}}} + \left|v_{\text{f},x}\right|}$$

$$(1.11e)\quad E\left(d_y^{\text{trav}} \middle| \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) \geq \bar{d}_y^{\text{f}}\right) = \frac{\left|v_{\text{f},x}\right| d_y^{\text{trav,max}}\, \bar{d}_y^{\text{f}}}{\left|v_{\text{v,v}} - v_{\text{v,f}}\right| \bar{d}_x^{\text{f}} + \left|v_{\text{f},x}\right| \bar{d}_y^{\text{f}}}.$$

Using eq. 1.11*c*:

$$(1.11f)\quad E\left(d_y^{\text{trav}} \middle| \left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) \geq \bar{d}_y^{\text{f}}\right) = \frac{\left|v_{\text{f},x}\right| \frac{\bar{d}_x^{\text{f}} \left|v_{\text{v},y} - v_{\text{f},y}\right|}{\left|v_{\text{f},x}\right|} \bar{d}_y^{\text{f}}}{\left|v_{\text{v,v}} - v_{\text{v,f}}\right| \bar{d}_x^{\text{f}} + \left|v_{\text{f},x}\right| \bar{d}_y^{\text{f}}}.$$

Simplifying, this becomes

$$(1.11g)\quad E(d_y^{\text{trav}} \mid v_{\text{f},x} \mid t(\bar{d}_y^{\text{f}}) \geq \bar{d}_y^{\text{f}}) = \frac{\left|v_{\text{v},y} - v_{\text{f},y}\right| \bar{d}_y^{\text{f}}}{\left|v_{\text{v,v}} - v_{\text{v,f}}\right| + \left|v_{\text{f},x}\right| \frac{\bar{d}_y^{\text{f}}}{\bar{d}_x^{\text{f}}}}.$$

This result is the same as that given in eq. 1.8*f* under $\left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) < \bar{d}_y^{\text{f}}$. Therefore, eq. 1.8*l* also holds under $\left|v_{\text{f},x}\right| t(\bar{d}_y^{\text{f}}) \geq \bar{d}_y^{\text{f}}$

Using eqs. 1.4 and 1.10, $E(\hat{D}_t \mid \hat{D}_t \neq 0)$ can be expressed by

$$(1.12)\quad E(\hat{D}_t \mid \hat{D}_t \neq 0) = E\left[\frac{D_{\text{f}}}{L} d_y^{\text{obs}}\right] = \frac{D_{\text{f}}}{L} \cdot \frac{\bar{d}_y^{\text{f}}\left|v_{\text{v},y}\right|}{\left|v_{\text{v},y} - v_{\text{f},y}\right| + \left|v_{\text{f},x}\right| \frac{\bar{d}_y^{\text{f}}}{\bar{d}_x^{\text{f}}}}.$$

The other component in the expression for $E[\hat{D}_t]$, $P[\hat{D}_t \neq 0]$, can be expressed as

$$(1.13)\quad P[\hat{D}_t \neq 0] = E\left[\frac{N_{\text{trans}}[\hat{D}_t \neq 0]}{T}\right] \equiv \begin{bmatrix}\text{fraction of } W \text{ in which}\\ \text{fish can be observed}\\ \text{during the survey}\end{bmatrix} = \frac{\left[d_x^{\text{obs}} \middle| d_x^{\text{trav}} = \bar{d}_x^{\text{f}}\right]}{W}$$

where $N_{\text{trans}}[\hat{D}_t \neq 0]$ is the number of transects in which fish are observed, T is the total number of transects, $[d_x^{\text{obs}} | d_x^{\text{trav}} = \bar{d}_x^{\text{f}}]$ is the distance in the x direction that fish can potentially be observed during the survey (i.e., the distance observed if the vessel were to traverse the distance across the fish in the x direction, $\bar{d}_x^{\text{f}}$), and W is the distance across the survey area in the x direction (Fig. A3).

$[d_x^{\text{obs}} | d_x^{\text{trav}} = \bar{d}_x^{\text{f}}]$ can be approximated by

$$(1.14)\quad \left[d_x^{\text{obs}} \middle| d_x^{\text{trav}} = \bar{d}_x^{\text{f}}\right] = \left|v_{\text{v},x}\right| t(\bar{d}_x^{\text{f}})$$

where $v_{\text{v},x}$ is the velocity vector of the vessel across the transects and $t(\bar{d}_x^{\text{f}})$ is the time it would take for the vessel to traverse the distance across the fish $\bar{d}_x^{\text{f}}$ in the x direction. $t(\bar{d}_x^{\text{f}})$ can be approximated by

$$(1.15)\quad t(\bar{d}_x^{\text{f}}) = \frac{\bar{d}_x^{\text{f}}}{\left|v_{\text{v},x} - v_{\text{f},x}\right|}.$$

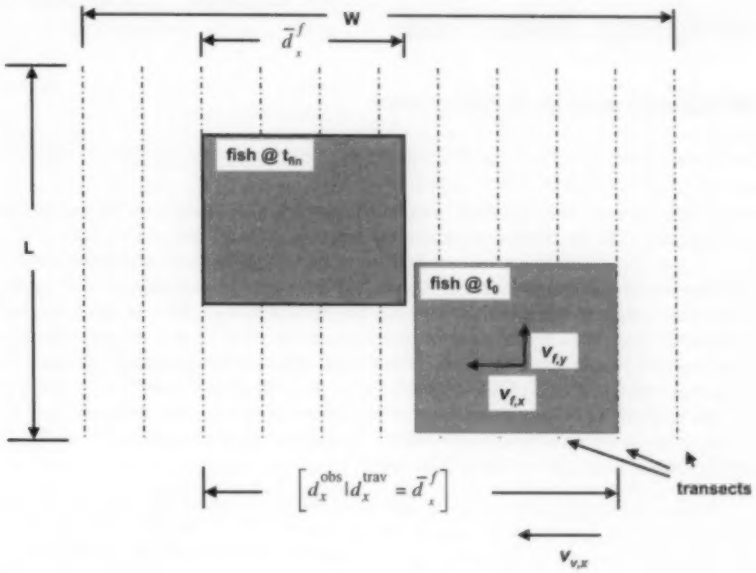
Therefore, by eqs. 1.13, 1.14, and 1.15, $P[\hat{D}_t \neq 0]$ can be approximated by

$$(1.16a)\quad P[\hat{D}_t \neq 0] = \frac{[d_x^{\text{obs}} | d_x^{\text{trav}} = \bar{d}_x^{\text{f}}]}{W} = \frac{\left|v_{\text{v},x}\right| t(\bar{d}_x^{\text{f}})}{W} = \frac{\left|v_{\text{v},x}\right| \bar{d}_x^{\text{f}}}{W\left|v_{\text{v},x} - v_{\text{f},x}\right|}$$

It should be noted that $P[\hat{D}_t \neq 0] \leq 1$ and therefore, by definition, $[d_x^{\text{obs}} | d_x^{\text{trav}} = \bar{d}_x^{\text{f}}] \leq W$. This is sensible because the ob-

© 1998 NRC Canada

Fig. A3. Schematic diagram showing the distance that a vessel would observe across the fish in the x direction between the begining and end of the survey if there is movement of fish in the x and y directions and the vessel travels the distance across the fish in the x direction. Fish @ t_0 refers to the position of the fish when the vessel first encounters the fish; fish @ t_{fin} refers to the position of the fish when the vessel exits the aggregation. See Appendix for an explanation.



servable distance of fish in the x direction can be no larger than the width of the survey area, W. Furthermore:

$$(1.16b)\quad P[\hat{D}_t \neq 0] \leq 1,\ \frac{|v_{v,x}|\bar{d}_x^f}{W|v_{v,x}-v_{f,x}|} \leq 1,\ \frac{|v_{v,x}|}{|v_{v,x}-v_{f,x}|} \leq \frac{W}{\bar{d}_x^f}.$$

This latter result is used below.

Using eqs. 1.1, 1.12, and 1.16*a*, $E[\hat{D}_t]$ can be expressed by

$$E[\hat{D}_t] = E[\hat{D}_t | \hat{D}_t \neq 0]P[\hat{D}_t \neq 0]$$

$$(1.17a)\quad = \frac{D_f}{L_T} \cdot \frac{\bar{d}_y^f |v_{v,y}|}{|v_{v,y}-v_{f,y}| + |v_{f,x}|\frac{\bar{d}_y^f}{\bar{d}_x^f}} \cdot \frac{|v_{v,x}|\bar{d}_x^f}{W|v_{v,x}-v_{f,x}|}.$$

This expression can be rearranged to

$$(1.17b)\quad E[\hat{D}_t] = \frac{D_f \bar{d}_y^f \bar{d}_x^f}{L_T W} \cdot \frac{|v_{v,y}|}{|v_{v,y}-v_{f,y}| + |v_{f,x}|\frac{\bar{d}_y^f}{\bar{d}_x^f}} \cdot \frac{|v_{v,x}|}{|v_{v,x}-v_{f,x}|}.$$

The first component on the right-hand side of this equation is equal to the mean density of fish in the survey area:

$$(1.17c)\quad D = \frac{D_f \bar{d}_y^f \bar{d}_x^f}{L_T W}.$$

Therefore, the equation for $E(\hat{D}_t)$ can be written

$$(1.17d)\quad E[\hat{D}_t] = D \cdot \frac{|v_{v,y}|}{|v_{v,y}-v_{f,y}| + |v_{f,x}|\frac{\bar{d}_y^f}{\bar{d}_x^f}} \cdot \frac{|v_{v,x}|}{|v_{v,x}-v_{f,x}|}.$$

© 1998 NRC Canada

Using Bayesian decision analysis to help achieve a precautionary approach for managing developing fisheries

M.K. McAllister and G.P. Kirkwood

Abstract: Bayesian decision analysis offers a useful framework for helping to achieve a precautionary approach to managing developing fisheries. With few data on the resource, data and experience from ecologically similar fish populations (or prior information) can also be used to quantitatively evaluate alternative procedures for managing the resource and to provide management advice. We applied Bayesian decision analysis to a hypothetical developing fishery in which a logistic model was fitted to catch per unit effort data. We evaluated the trade-offs in yield and the risk of depletion of catch and effort control rules. Effort control rules yielded average catches nearly 40% larger for levels of risk similar to those given by catch control rules. Management procedures designed to reduce the risks of implementing high harvest rates and to promote resource recovery at low stock sizes reduced the risks of overexploitation and caused only very small reductions in average catch. However, –50 and +100% biases in prior probability distributions for some parameters and the use of overly precise priors (CV < 0.5) in stock assessments caused large increases in the risk of overexploitation.

Résumé : L'analyse bayesienne offre un cadre utile pour mettre en oeuvre une approche prudente dans la gestion des pêches en développement. Lorsqu'on dispose de peu de données sur la ressource, on peut tirer profit de l'information et de l'expérience obtenues avec des populations écologiquement semblables (ou utiliser des a priori) pour évaluer quantitativement diverses méthodes de gestion de la ressource et pour donner des conseils de gestion. Nous avons appliqué l'analyse bayesienne à une pêche en développement hypothétique dans laquelle un modèle logistique a été ajusté aux données sur les captures par unité d'effort. Nous avons évalué les compromis entre la production et le risque d'appauvrissement de la ressource selon les règles de contrôle des captures et de l'effort. Les règles de contrôle de l'effort donnaient des captures moyennes de près de 40% supérieures, pour des niveaux de risque similaires, à celles obtenues avec les règles de contrôle des captures. Les méthodes de gestion conçues pour réduire les risques d'établissement de taux de capture élevés et pour promouvoir le rétablissement de la ressource quand l'effectif est faible abaissent les risques de surexploitation et ne causaient que de très faibles réductions des captures moyennes. Toutefois, les biais de –50 et de +100% dans les distributions a priori de distribution de certains paramètres et l'emploi d'a priori trop précis (CV < 0,5) dans les évaluations des stocks ont causé de fortes augmentations du risque de surexploitation.

[Traduit par la Rédaction]

Introduction

Despite the increasing occurrence of overexploitation (harvesting at levels higher than maximum sustainable yield (MSY)) among commercially valuable fish stocks, a recent Food and Agriculture Organization of the United Nations (FAO) report suggested that 31% of the world's fish stocks remain underexploited to moderately exploited with potential for further development (Garcia and Newton 1994). Many of the most valuable of these are deepwater resources with relatively little scientific work on their biology. The situation faced by fishery managers in such developing fisheries is a classic example of decision making under uncertainty. With relatively little information available about the abundance and biology of the resource, managers face difficult decisions over the amount of fishing to allow in the initial years of development. On the one hand, allowing high harvesting rates could heavily deplete the resource before sufficiently precise abundance estimates could be obtained to make this depletion evident. On the other hand, allowing low harvesting rates could prevent observable changes in stock size and lead to chronic underexploitation (Smith 1993).

Bayesian decision analysis and Monte Carlo Bayesian methods have recently been advocated for stock assessment and the evaluation of alternative fishery management procedures (e.g., Bergh and Butterworth 1987; McAllister et al. 1994; Punt and Hilborn 1997; McAllister and Kirkwood 1998). These methods are particularly appropriate for guid-

Received July 24, 1997. Accepted August 4, 1998.
J14134

M.K. McAllister[1] and G.P. Kirkwood. Renewable Resources Assessment Group, Centre for Environmental Technology, T.H. Huxley School of the Environment, Earth Science, and Engineering, 8 Prince's Gardens, South Kensington, London, SW7 1NA, U.K.

[1]Author to whom all correspondence should be addressed. e-mail: m.mcallister@ic.ac.uk

© 1998 NRC Canada

ing management actions in developing fisheries. In addition to using regular stock assessment data, the methods allow experience and data from similar fish populations to be incorporated into the evaluation of alternative fishery management procedures in the form of prior distributions. The approach also provides effective methods to account for and communicate uncertainties.

In this paper, we provide a Bayesian decision analytic framework for evaluating alternative fishery management procedures that could be applied in a developing fishery. We exemplify the decision analytic framework in manner consistent with guidelines for a precautionary approach to managing developing fisheries (FAO 1995; see Appendix 1 for a summary of some of these guidelines). We apply the framework to evaluate alternative management procedures in a hypothetical developing fishery. The procedures consist of sets of quantitative decision rules that are strictly followed in each year of management. Adherence to such rules by fishery managers and the fishing industry, provided that the rules have been thoroughly evaluated under a wide variety of conditions, has been favoured by some (FAO 1995; Butterworth et al. 1997). This is because it reduces time-consuming and expensive annual debates over the setting of annual harvest controls and can provide a systematic approach to improving overall management performance.

Fishery management procedures can consist of sets of decision rules that determine the total annual allowable catch (TAC), total amount of annual fishing effort, the types of stock assessment methods, and the data collection strategies to be applied. The decision rules used to set or adjust catches can be referred to as catch control rules. Similarly, the rules that are used to set the amount of effort are referred to as effort control rules. Parameters used to adjust catch or effort are referred to as policy tuning parameters.

The example in this paper addresses some key issues regarding the evaluation of alternative management procedures for developing fisheries. Firstly, concerns have recently been raised over the effectiveness of fishery management procedures that attempt to directly control the total catches removed from a fishery resource (i.e., that apply catch control rules) (Walters and Maguire 1996). This is mainly because of the high costs of acquiring data of sufficient accuracy and precision to implement harvesting control procedures effectively. Other management approaches, such as those that attempt to control the total amount of fishing effort, could potentially be more robust to inaccurate and imprecise data. We therefore evaluate the potential consequences of alternative fishery management procedures that apply catch versus effort control rules, based on stock assessments of catch and effort data.

Secondly, a further problem with implementing management procedures based on imprecise or few data is that there may be a high risk of allowing very high harvest rates (Frederick and Peterman 1995). We take harvest rate to mean the fraction of catch biomass to harvestable stock biomass. We present some catch and effort control rules that can be applied to reduce the risk of allowing high harvest rates when there is little information available. Other catch and effort control rules are presented that could be applied to promote resource recovery when low resource levels are detected.

Thirdly, previous work has indicated that results from the evaluation of management procedures can be sensitive to the prior distributions used for input parameters, especially when data are relatively uninformative (McAllister et al. 1994; Walters and Ludwig 1994; McAllister and Kirkwood 1998). This can be a major problem if priors are biased, for example, if priors are centered about values that are higher or lower than the actual values or the stock assessment model strongly misrepresents the actual situation. The effects of biased priors may be particularly severe in developing fisheries, since few data are typically available about the resource in the initial years of exploitation. In this paper, we evaluate the sensitivity of decision analysis results to instances in which priors for model parameters are misspecified.

To make the problem worse, priors can also be too sharply concentrated about an incorrect value. Several authors have noted a common tendency for priors constructed using expert judgment to be overly confident and far too precise (Berger 1985; Walters and Ludwig 1994). In other instances, some parameters, for example, stock–recruit parameters, may be estimated assuming less precise prior information than that given by data from similar populations. We therefore evaluate the expected consequences of using priors that are centered too high or too low or are too sharp or too flat.

When posteriors are relatively diffuse and skewed, the control implemented can depend strongly on whether the mean, median, or mode of the distribution is applied in the management procedure. We therefore evaluate the effects on policy performance of using the mean, median, and mode of posteriors used in the decision analyses.

In order to keep the analysis at a fairly general level, a stochastic biomass dynamic model was used to simulate the population dynamics. In the management procedures evaluated, only a deterministic biomass dynamic model that was fitted to simulated catch per unit effort (CPUE) data was considered for stock assessment.

A Bayesian framework to evaluate fishery management procedures

General frameworks for Bayesian stock assessment and decision analysis have been presented in McAllister et al. (1994), Punt and Hilborn (1997), McAllister and Pikitch (1997), and McAllister and Kirkwood (1998). Below, we summarize the steps required to evaluate fishery management procedures.

(1) Identify each alternative management procedure. The set of alternative management procedures that could be taken is usually identified through discussions among fishery managers, scientists, and industry members.
(2) Specify the indices of policy performance. The most desirable policy option for fishery managers is often the one that has the largest expected economic benefits and has an acceptably high chance of avoiding undesirable biological and economic outcomes. This step thus involves defining (*a*) a set of indices with which to evaluate policy performance and (*b*) a time horizon over which to evaluate the potential outcomes of each policy. Indices that are often chosen include measures of the

© 1998 NRC Canada

expected average catch biomass, interannual variability in catch biomass, and probability of depleting the stock below some threshold (Bergh and Butterworth 1987).

(3) Specify the alternative hypotheses. To evaluate the consequences of alternative management procedures in a developing fishery, a single population dynamics model could be formulated to describe the population dynamics of the newly discovered resource. This model would be used to predict the consequences of alternative management procedures. Such models are often referred to as "operating models" (Punt 1997). The policy that performs best may depend strongly on the values used for the model's parameters, and there is often considerable uncertainty over the values that best describe the actual population dynamics. In Bayesian decision analysis, it is common to account for such uncertainty by treating the alternative values for model parameters as alternative hypotheses and calculating the consequences of each management procedure under each alternative hypothesis (Berger 1985). Incorporating structurally different models for population dynamics as alternative hypotheses could also be useful, but only once fishery scientists are able to provide compelling conjectures about structurally different alternatives (e.g., regarding migration and recruitment).

(4) Determine the relative weight of the evidence in support of the alternative hypotheses. This step has at least two stages. The first is to construct a prior distribution (or prior), $p(\theta)$, for all uncertain model input parameters (e.g., parameters r and K in the logistic model, denoted jointly as the vector θ, see below). The prior conveys the relative credibility of alternative parameter values before evaluating the stock assessment data for the resource of interest. Data and experience from managing other similar populations can be used to construct such priors. The second step is to combine the priors and the stock assessment data using Bayes' theorem to estimate the posterior probability distribution (or posterior) for model input parameters. The posterior distribution $P(\theta|\text{data})$ summarizes the weight of the evidence in support of the alternative hypotheses.

(5) Evaluate the distribution and expected value of each management performance measure for each alternative management procedure. This usually involves the following steps: (*a*) randomly draw values for parameters from their posterior distribution (e.g., r and K in the logistic model; see eq. 1 below), (*b*) using the drawn parameter values, project the model into the future under the management procedure of interest (recall that this could involve simulating future stock assessments to set, e.g., annual TACs), (*c*) calculate the outcomes of the management procedure in this single future projection, (*d*) repeat steps *a* to *c* many times, and (*e*) produce a distribution of outcomes for the management procedure. The same draws are used when comparing performance across management procedures. It is also important to note that the process error terms are included in a draw.

(6) Present the results to decision makers. Summarize results for each management procedure in the form of probability distributions and expected values.

Evaluating alternative harvest control rules using the logistic model

We applied the decision analytic approach outlined earlier to evaluate the potential consequences of implementing alternative catch control and effort control rules in a hypothetical developing fishery. In order to keep the analysis at a fairly general level, we used a very simple population dynamics model, the logistic model, in the decision analysis and simulated stock assessments. We begin by describing the operating model because key components of all of the other steps are determined by it.

Operating model: population dynamics and parameter specification

In the decision analysis, we applied a stochastic discrete-time version of the logistic model as the operating model to represent population dynamics of the newly discovered resource:

$$(1) \qquad B_{y+1} = \left[B_y + rB_y\left(1 - \frac{B_y}{K}\right)\right] e^{\varepsilon_y - \frac{\sigma_o^2}{2}} - C_y$$

where y is the year, B is stock biomass, r is the intrinsic rate of increase, K is the carrying capacity, C is the catch biomass, $\varepsilon_y \sim \text{Normal}(0, \sigma_o^2)$, and σ_o is the lognormal standard deviation (SD) or approximate coefficient of variation (CV) in the "process" error about the logistic model. The baseline value for σ_o was 0.1. The C_y was assumed to be equal to the realized catch for the year. The maximum harvest rate possible was assumed to be 0.9. Therefore, the simulated catch was set to a value equal to 90% of stock biomass if the actual harvest rate (C_y/B_y) was to exceed 0.9. To simulate the beginning of management under nonequilibrium conditions, the stock biomass was set to K, 20 years before the initiation of management and biomass varied lognormally in each of the years over this period (eq. 1).

In a Bayesian decision analysis of alternative harvest policies, probability distributions for model parameters can be applied in at least two ways: (1) as a posterior distribution to indicate the weight of all available evidence in support of alternative hypotheses in the decision analysis (step 4 above) and (2) as a prior distribution to increase precision in parameter estimates in simulated future stock assessments (step 5*b* above). In decision analysis, the posterior distribution specifies the set of alternative hypotheses over which to evaluate the consequences of alternative management procedures and reflects the relative probability that each hypothesis is true. The consequences of alternative management procedures are thus evaluated over the full range of these alternative hypotheses, and the posterior distribution is used to weight the potential outcomes of each management procedure under each hypothesis.

For posterior distributions to be useful for decision analysis (step 4 above), it is usually necessary that they are informative for the alternative hypotheses that are considered (e.g., the marginal posterior distribution for any of the parameters cannot be uniform over an infinite range of values). Otherwise, problems could be encountered, for example, in the numerical integration. Furthermore, the distribution of outcomes could also be flat over an infinite range and non-

© 1998 NRC Canada

sensical. Such results would be of little use to decision makers.

The alternative hypotheses considered in this decision analysis consisted of alternative values for the parameters r, K, and q (the catchability coefficient, see below). For our analysis, we assumed that by the initiation of the first decision analysis of alternative management procedures, sufficient information already existed to obtain an informative posterior distribution for the population model parameters. This distribution could have been obtained, for example, from a preliminary stock assessment that used commercial catch and effort data that were available from exploratory fishing operations and a research survey of initial abundance. Furthermore, informative priors for parameters, such as r, could have been formulated by analyzing data for other ecologically or taxonomically similar populations (Gelman et al. 1995) and used in the preliminary stock assessment to produce the posterior distribution for the decision analysis. Note that the posterior distribution for parameters used in step 4 of the decision analysis above can sometimes also be applied in step 5*b* above: this posterior distribution could also be applied in future stock assessments as the prior distribution and combined with data obtained from the application of the management procedure.

In all cases, we applied joint posterior (step 4 above) and prior distributions (step 5*b* above) for model parameters that assumed that the model parameters were independent, i.e., no covariance was assumed among model parameters in these distributions. Note that this is a more conservative assumption about the amount of information available than if dependence had been assumed. The baseline marginal probability distributions used to weight alternative values for parameters r, K, and q (see below) were as follows:

$$r \sim \text{lognormal}(0.4,\ 0.5^2)$$

$$K \sim \text{lognormal}(1000,\ 0.6^2) \quad (2)$$

$$q \sim \text{lognormal}(0.1,\ 0.6^2).$$

The distribution for r represents a range of values consistent with a wide variety of gadoids, lutjanids, scombrids, flatfishes, and longer-lived clupeids. Although the distributions are relatively flat, they do convey some information. For example, a 95% probability interval for r is 0.15–1.06. A 95% probability interval for K is 310–3243. A 95% probability interval for q is 0.031–0.32.

Simulated data

The management procedures that were evaluated were based on harvest control rules that were applied to the simulated results of a simple stock assessment procedure (see below for details). The stock assessment procedure fitted a deterministic biomass dynamic model (eq. 1 with σ_ω set to 0) to simulated CPUE and catch data. Therefore, the model for resource dynamics required the simulation of CPUE and catch data.

CPUE data

In most developing fisheries, fishers become more efficient at catching fish as they learn more about the resource and implement more effective methods of capture. These increases in catching power pose problems for stock assessment because of the common but unlikely assumption that catchability remains constant over time. In our baseline evaluations, we therefore assumed that harvest management was not implemented until this initial learning period was finished. The catches taken in this initial period were assumed to be negligible.

Simulated CPUE data in each year y were assumed to be directly proportional to stock biomass and lognormally distributed about their true values:

$$I_y^c = qB_y e^{\nu_y, \omega_y - \sigma_E^2/2} \quad (3)$$

where q is the true catchability coefficient, σ_E is the true SD in the logarithm of observed CPUE data that results from sampling error and interannual variability in q, and ν_y and ω_y are independent random normal deviates from sampling error and interannual variability in q, respectively: $\nu_y \sim$ Normal(0, σ_ν^2), $\omega_y \sim$ Normal(0, σ_ω^2), and $\sigma_E^2 = \sigma_\nu^2 + \sigma_\omega^2$. The baseline values for σ_ν and σ_ω were 0.2 and 0.1, respectively.

We caution that the first assumption about CPUE data above may be unreasonable for a variety of reasons. For example, as indicated before, q may increase temporally as fishers become more knowledgeable about the resource and how to exploit it, and q may also be a nonlinear function of stock size. We apply the assumption because it is simple and makes the illustration easier.

Catch data

The method used to simulate catch data depended on the type of harvest control rule evaluated. Two types of harvest control rules were considered: (1) catch control in which the annual TAC was assumed to be taken each year and measured without error (i.e., $C_y = \text{TAC}_y$) and (2) effort control in which the target level of effort (e.g., vessel days per year) was assumed to be implemented and observed without error in each year. The actual catch was assumed to be a function of the actual level of effort, E_y (see below), catchability, q, and stock biomass, B_y:

$$C_y = q E_y B_y e^{\omega_y - \sigma_\omega^2/2}. \quad (4)$$

The actual level of effort was assumed to be equal to the target level of effort, E_y^T unless the harvest rate implied by E_y^T exceeded 0.9 (see below). Catch biomass was assumed to be measured without error. In contrast, the CPUE data were assumed to be measured with error and lognormally distributed as in eq. 3.

Management procedures considered

The management procedures considered included an estimator, a protocol for collecting data, and a set of rules for controlling the harvest of fish. The second of these was held constant while we evaluated several alternative harvest control rules and the use of different prior distributions in the estimator.

Estimator

A Bayesian estimator was applied in all management procedures evaluated. This required a population dynamics model, a likelihood function, and prior distributions for stock assessment model parameters. In each simulated annual stock assessment, the deterministic version of eq. 1

© 1998 NRC Canada

($\sigma_o = 0$) was fitted to catch rate data. In the estimation, catch rates were assumed to be directly proportional to stock size and lognormally distributed:

$$(5) \qquad I_y^c \sim \text{lognormal}(\hat{q}\hat{B}_y, \sigma_S^2)$$

where $\hat{q}\hat{B}_y$ is the product of the estimated quantities for catchability and stock biomass in year y given by the stock assessment model and σ_S is the SD of the logarithm of the catch rate data that are used in the simulated stock assessment.

The log likelihood function, λ, of the catch rate data is therefore given by

$$(6) \qquad \lambda = -\frac{0.5}{\sigma_S^2}\sum_{y=1}^{n}\left[\log\left(\frac{I_y^c}{qB_y}\right)\right]^2 - n\log\sigma_S + \text{const}$$

where $y = 1$ corresponds to the first year of the catch rate time series, const is a constant value, and n is the length of the catch rate time series. Normally, σ_S would be estimated. However, due to the short time series, especially in the initial years of management, σ_S would be very imprecisely estimated. Usually, about 30 data points are required to estimate an SD with reasonable precision. Furthermore, the value for σ_S determines the relative weight of the data and the priors in the estimation of model parameters. If data are few, presetting the value for σ_S can avoid undue weighting of either. Therefore, the value for σ_S was not estimated but was fixed at its expected value resulting from observation error and process error:

$$(7) \qquad \sigma_S = \sqrt{\sigma_E^2 + \sigma_o^2}.$$

Estimation failure was assumed to have occurred when posterior parameter estimates were outside of preset ranges. For r, the range was 0.01–1.2. For q, it was 0.01–10. For K, it was 0–8000. For B_y, the lower bound of the range was 0.025 of the estimate of K. When an estimation failure was detected, the results of the estimation in that particular year were ignored in the evaluation of estimation performance. The parameter estimates were then set at their prior modal values.

In each stock assessment, the quantities r, K, q, B_y, MSY, and the effort and harvest rate at MSY were estimated. The posterior modal values for these quantities were used as inputs to the harvest control rules. These were used to set TACs or effort, depending on the management procedure evaluated.

Prior distributions used in estimators

In Bayesian stock assessments, the prior distribution used for model parameters can reflect what is known about the credibility of alternative parameter values apart from the information contained in the stock assessment data. However, the prior distribution, if it is informative, can also be used together with the stock assessment data (e.g., catch and effort data) obtained while implementing the management procedure to help estimate the population model parameters. Informative priors can be particularly helpful in stock assessments of developing fisheries when data are relatively uninformative (McAllister et al. 1994). However, as noted earlier, priors applied in stock assessments can potentially be biased and also too precise. This bias can also occur in conventional stock assessments when the value for a key parameter (e.g., the rate of natural mortality) in a stock assessment model is fixed at some particular value and assumed correct when it is really not (Lapointe et al. 1989). The potential consequences of using priors that are too precise have received relatively little attention. Therefore, we consider below the case in which the prior used in a stock assessment is too precise relative to the uncertainties represented by the posterior distribution in the decision analysis.

In the simulated stock assessments, various informative priors were considered for parameters K, r, and q. The baseline prior is given in eq. 2. As mentioned before, an informative prior for these three parameters is conceivable: a posterior distribution obtained from a preliminary stock assessment of data from exploratory fishing, a research survey, and similar populations could be applied as the prior distribution in future stock assessments.

Harvesting control rules

The above decision analysis procedure was applied to evaluate the consequences of implementing a variety of harvest control rules that included both catch control and effort control rules.

Catch control rules

Two sets of MSY-based policies were considered. The first set of policies was based on the estimated MSY harvest rate:

$$(8) \qquad Q_y = p h_{\text{MSY}} \hat{B}_y$$

where

$$(9) \qquad h_{\text{MSY}} = \frac{\hat{r}}{2}$$

and $\hat{B}_y$ is the estimate of biomass in year y, $\hat{r}$ is the (e.g., posterior modal) estimate of r, p is a policy tuning parameter that is some fixed fraction (e.g., 0.5, 0.75, or 1), and Q_y is the catch quota. The p determines the intensity of the harvest rate to be applied and is analogous to the $0.n$ in $f_{0.n}$ from yield per recruit analysis. This management procedure could lead to quite large values for Q_y in the first few years because a fixed fraction of the biomass is taken as the stock is fished down (see Fig. 3). It is also expected to result in a decrease in Q_y and catch rates as stock biomass is depleted.

The second series of policies is based on the estimated MSY:

$$(10) \qquad Q_y = p\text{MSY} = p\frac{\hat{r}\hat{K}}{4}$$

where $\hat{K}$ is the estimated carrying capacity and p is also a policy tuning parameter.

In all cases, a constraint on the maximum allowable amount of change in quota between years was implemented. The quota was allowed to change by no more than 25% from one year to the next (i.e., a 25% decision rule). This constraint was not applied in the first year of the management procedure. This was in order to address practical con-

© 1998 NRC Canada

siderations regarding the ability of fishing capacity to expand or contract from year to year.

Decision rules for setting a maximum TAC Because of uncertainties in parameter estimates, there is a risk that the estimated TAC will be far too large, especially in the first few years of management when data are few. This actually occurred for several of the policies evaluated (see below). With the use of posterior distributions for model parameters, an upper limit to the TAC, TAC_y^*, can be specified such that it yields an acceptably low probability of exceeding a prespecified threshold harvest rate, HR*. The TAC can then be set to this TAC_y^* if the target TAC exceeds TAC_y^*.

If estimates of the model parameters (e.g., r, K, q) are approximately lognormally distributed, then the calculation of TAC_y^* becomes trivial. For example, if the estimate of B_y from a stock assessment is lognormal($\mu_{B_y}, \sigma^2_{B_y}$), where μ_{B_y} is the median of the marginal posterior for B_y, then the harvest rate TAC_y^*/B_y is lognormal($TAC_y^*/\mu_{B_y}, \sigma^2_{B_y}$). If a threshold probability, P^*, is specified, then the problem can be formulated by finding the maximum TAC that gives

$$P(\mathrm{HR} > \mathrm{HR}^*) < P^*$$

Log-transforming, we have

$$P(\log[\mathrm{HR}] > \log[\mathrm{HR}^*]) < P^*$$

and because log[HR] is normally distributed:

$$(11a)\quad z^* = \frac{\log(\mathrm{HR}^*) - \log\left(\dfrac{\mathrm{TAC}_y^*}{\mu_{B_y}}\right)}{\sigma_{B_y}}$$

where z^* is a value in the $Z \sim$ Normal(0, 1) distribution such that $P(Z > z^*) = P^*$. After rearranging eq. 11*a*:

$$(11b)\quad \mathrm{TAC}_y^* = \mathrm{HR}^* \mu_{B_y} \exp[-z^* \sigma_{B_y}]$$

Therefore, TAC_y^* can be calculated providing that HR*, μ_{B_y}, z^*, and σ_{B_y} are specified. The μ_{B_y} can be obtained from the estimate of the posterior median value for B_y in the simulated stock assessment. The σ_{B_y} was approximated using the delta method and a numerical estimate of the Hessian matrix (Appendix 2).

The use of eq. 11*b* can be exemplified as follows. If in the first year of management, we set HR* to 0.5 and P^* to 0.01 (i.e., $z^* = 2.33$) and use the baseline prior for K (i.e., $K \sim$ lognormal(1000, 0.6^2)), then TAC_y^* is 124. Under the MSY quota management procedure, the modal estimate of the TAC is 54. As this is less than TAC_y^*, the TAC in the first year is set to 54. Under the MSY harvest rate management procedure, the modal estimate of the TAC is 110, and the TAC is therefore set to 110. Alternative values for HR* were evaluated to identify policies with acceptably low risks of depletion but reasonably high yields. This decision rule is referred to as the harvest rate cap rule.

Catch control rules for when low stock sizes are detected When the catch control rules above were applied unchanged when stock sizes were depleted below $0.5K$, further implementation of the rules tended to drive the population to very low levels. Therefore, the following catch control rule was applied when low stock size was detected. If the estimate of B_y was less than $0.5\hat{K}$, the product of the estimated quota and a second factor was taken until the estimate of biomass exceeded $0.5\hat{K}$:

$$(12)\quad \text{If } \hat{B}_y < 0.5\hat{K}, \text{ then } \mathrm{TAC}_y = Q_y\left(\frac{\hat{B}_y}{0.5\hat{K}}\right)^{\alpha}$$

where $\alpha > 0$. This was called the resource recovery rule. An analogous rule was needed for low stock size under the effort control rule (see below).

Summary of catch control rules The following equations summarize the catch control rules for the harvest rate and MSY quota control rules:

$$(13)\quad \mathrm{TAC}_y = \begin{cases} 0.75C_{y-1} & \text{if } Q_y < 0.75C_{y-1} \\ Q_y & \text{if } 0.75C_{y-1} \le Q_y \le 1.25C_{y-1} \\ 1.25C_{y-1} & \text{if } Q_y > 1.25C_{y-1} \end{cases}$$

For the harvest rate rule:

$$(14a)\quad Q_y = \min(\mathrm{HR}_y \hat{B}_y, \mathrm{HR}^* e^{-z^* \sigma_{B_y}} \hat{\mu}_{B_y})$$

$$(14b)\quad \mathrm{HR}_y = \begin{cases} p\dfrac{\hat{r}}{2} & \text{if } \hat{B}_y \ge 0.5\hat{K} \\ p\dfrac{\hat{r}}{2}\left(\dfrac{\hat{B}_y}{0.5\hat{K}}\right)^{\alpha} & \text{if } \hat{B}_y < 0.5\hat{K}. \end{cases}$$

For the MSY quota rule:

$$(15a)\quad Q_y = \min(Q_y'', \mathrm{HR}^* e^{-z^* \sigma_{B_y}} \hat{\mu}_{B_y})$$

$$(15b)\quad Q_y'' = \begin{cases} p\dfrac{\hat{r}\hat{K}}{4} & \text{if } \hat{B}_y \ge 0.5\hat{K} \\ p\dfrac{\hat{r}\hat{K}}{4}\left(\dfrac{\hat{B}_y}{0.5\hat{K}}\right)^{\alpha} & \text{if } \hat{B}_y < 0.5\hat{K} \end{cases}$$

Effort control rules

In several situations, it may be desirable to set management controls on the total amount of fishing effort allowed in a fishery. This could help to reduce the chances of excessive fishing effort building up as management progresses and could be less sensitive to uncertainty in the data than implementing a catch control rule. For example, in contrast with harvest rate control rules, effort control rules do not require estimates of biomass. Therefore, MSY-based effort control options were evaluated. In each year, the MSY effort level was estimated and the target effort E_y^{T} was some fraction of this effort at MSY:

$$(16)\quad E_y^{\mathrm{T}} = p\hat{E}_{\mathrm{MSY}} = p\frac{\hat{r}}{2\hat{q}}$$

where p is a policy tuning parameter (eq. 8), $\hat{E}_{\mathrm{MSY}}$ is the estimated effort at MSY, $\hat{r}$ is the estimate of r, and $\hat{q}$ is the estimate of q. The actual effort, E_y, was assumed to be equal to

© 1998 NRC Canada

E_y^T unless the harvest rate, qE_y^T, exceeded 0.9. If the harvest rate exceeded 0.9, then E_y was set to $0.9/q$, where q is the true simulated value for catchability. The E_y was then applied in eq. 4 to generate actual annual values for catch biomass. As with the catch control rules, a constraint on the maximum allowable change in target effort between years was considered. The target effort was allowed to change by no more than 25% from one year to the next.

Decision rules for setting a maximum allowable effort

Analogous rules to those used under the catch control rules were used to set maximum allowable values for effort. The effective target harvest rate, HR^e, under effort control was given by

$$(17a) \quad HR^e = E_y^T q$$

where E_y^T is the target effort and q is the true simulated value for q. Because the posterior for q from a stock assessment is lognormal (μ_q, σ_q^2), then HR^e is lognormal $(E_y^T\mu_q, \sigma_q^2)$. Note that if σ_q^2 is large, then very large values for HR^e can result. If a threshold value for the maximum allowable harvest rate and an acceptably low value for the probability P^* that the real harvest rate exceeds this value are specified, then the following equation can be used to obtain the maximum allowable effort:

$$(17b) \quad E_y^* = \frac{HR^*}{\mu_q} \exp[-z^*\sigma_q].$$

The value for μ_q was obtained each year from the posterior median q and the value for σ_q was obtained from the inverse Hessian. Under the baseline priors and values for HR^* and P^* of 0.5 and 0.01, respectively, E_y^* becomes 1.23 in the initial year of management. However, the prior modal estimate of E_y^T was 2.23. Therefore, the target effort was set to 1.23 in the initial year of management.

Effort control rules for when low stock sizes are detected

The following effort control rules were applied when low stock size was detected. If the estimate of biomass in a given year was less than $0.5\hat{K}$, the target effort was set to the product of the estimated effort and a second factor taken until the estimate of biomass exceeded $0.5\hat{K}$:

$$(18) \quad \text{If } \hat{B}_y < 0.5\hat{K}, \text{ then } E_y^T = p\frac{\hat{r}}{2\hat{q}}\left(\frac{\hat{B}_y}{0.5\hat{K}}\right)^{\alpha}$$

where $\alpha > 0$.

Summary of effort control rules The following equations summarize the effort control rules:

$$(19a) \quad E_y = \begin{cases} 0.75E_{y-1} & \text{if } E_y^T < 0.75E_{y-1} \\ E_y^T & \text{if } 0.75E_{y-1} \le E_y^T \le 1.25E_{y-1} \\ 1.25E_{y-1} & \text{if } E_y^T > 1.25E_{y-1} \end{cases}$$

$$(19b) \quad E_y^T = \min\left(E_y^{T'}, \frac{HR^*}{\mu_q}\exp[-z^*\sigma_q]\right)$$

$$(19c) \quad E_y^{T''} = \begin{cases} p\dfrac{\hat{r}}{2\hat{q}} & \text{if } \hat{B}_y \ge 0.5\hat{K} \\ p\dfrac{\hat{r}}{2\hat{q}}\left(\dfrac{\hat{B}_y}{0.5\hat{K}}\right)^{\alpha} & \text{if } \hat{B}_y < 0.5\hat{K} \end{cases}$$

Measures of policy performance

The following measures of policy performance were computed for each management procedure: (1) the average catch over the time horizon (e.g., 30 years for a relatively short-lived life history type), (2) the average annual percent change in the catch, (3) the average annual percent change in the effort, (4) the depletion (*a*) in each year and (*b*) in the final year (B_{fin}/K), (5) the proportion of simulation that the biomass falls below $0.2K$ (*a*) at any time in the management horizon and (*b*) in a given year, (6) the average percent bias in the estimates of r, K, q, biomass, MSY, and other quantities in the final year, and (7) the average percent absolute deviation between the estimated and true target quantity to be controlled (e.g., MSY, effort at MSY) in the final year. The average annual percent change in a quantity Y was obtained from

$$\%|\Delta Y| = \frac{100\%}{m}\sum_{i=1}^{m}\sum_{y=2}^{n}\frac{|Y_{i,y} - Y_{i,y-1}|}{Y_{i,y-1}}$$

where $Y_{i,y}$ is the true value for the quantity in year y for projection i, n is the length of the evaluation horizon, and m is the number of draws taken randomly from the joint posterior for r, K, and q. The percent expected mean absolute error (%EMAE(X)) for quantity X was obtained from

$$\%\text{EMAE}(X) = \frac{100\%}{m}\sum_{i=1}^{m}\frac{|\hat{X}_i - X_i^{\text{true}}|}{X_i^{\text{true}}}$$

where $\hat{X}_i$ and X_i^{true} are the estimated and true simulated values for quantity X in simulation i; m = 800 draws from the joint posterior distribution for r, K, and q were taken to compute distributions for the policy performance indicators.

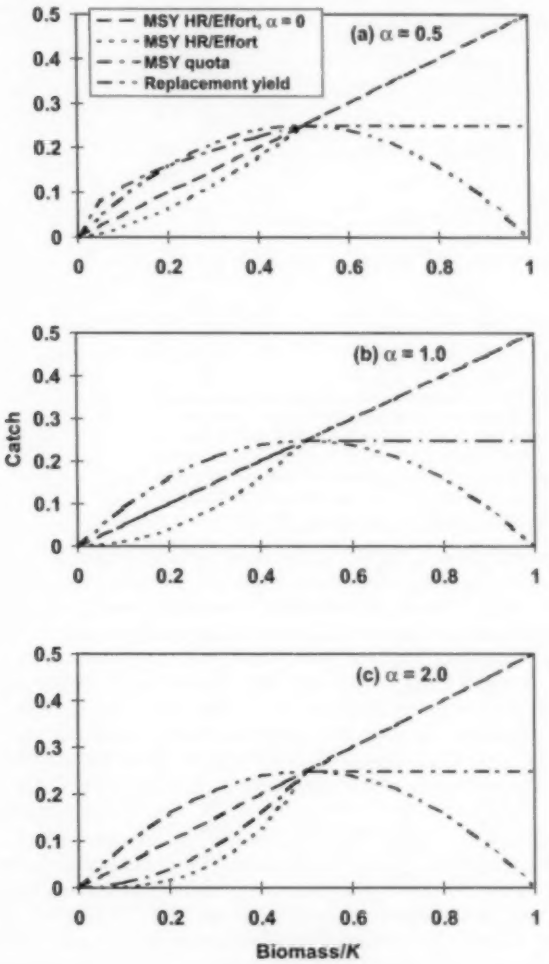
Evaluating the effects of biases in prior distributions on expected policy performance

As noted earlier, the results of a decision analysis can depend strongly on the prior distributions applied in the management procedures evaluated, especially when data are not very informative, as in developing fisheries. The effects of the biases in priors can also potentially be affected by the precision in the posterior distribution used to weight alternative hypotheses in the decision analysis. Therefore, once a relatively high-performance management procedure was identified under baseline conditions, we evaluated the following situations.

(1) Using priors that are positively or negatively biased. In this case, we evaluated the effects on policy performance of applying priors in stock assessments that are positively or negatively biased relative to the posterior distribution used to weight alternative states of nature in the decision analysis. Priors for r, K, and q were considered that had medians that were either 50% too small or

© 1998 NRC Canada

Fig. 1. Deterministic relationships between catch and stock size relative to K for the MSY harvest rate, effort control, and quota management procedures. Results are shown for $\alpha = 0$, (*a*) $\alpha = 0.5$, (*b*) $\alpha = 1.0$, and (*c*) $\alpha = 2.0$. The replacement yield is also shown.



100% too large relative to the medians of the marginal posteriors used in the decision analysis.

(2) Using highly informative versus overly diffuse priors. Two alternative scenarios were considered. In the first, the prior distributions used in the future simulated stock assessments were identical to the marginal posterior distributions in the decision analysis, as is commonly assumed in Bayesian evaluations, i.e., the stock assessments in each management procedure started out with the prior estimates of parameters and were subsequently updated as more data were obtained in subsequent years. It would seem plausible that as a posterior distribution in a decision analysis becomes more precise about a median value that is not pessimistic, the expected risks of the various feedback policies should decrease. This may not be the case, however, if the priors in the stock assessment are overly precise relative to the actual amount of uncertainty. This latter situation is typical in fishery management: more certainty is often assumed in the stock assessment than is supported by available data and experience. To illustrate the effects on policy performance of starting out with priors that are too precise, we evaluated a second situation in which the priors in the stock assessment only were overly precise relative to the posterior used in the decision analysis.

Bayesian estimators used in the harvesting control rules

Decision rules applied in feedback policies require estimates of model quantities. These can be based on the mode, mean, or median of the posterior distribution for each quantity. Policy performance can sometimes depend on the mode, median, and mean (Cordue and Francis 1994) if the distribution is skewed. A commonly used Bayes estimator is the posterior expectation (Berger 1985). In models with several uncertain parameters (e.g., three or more), calculation of this quantity can be time consuming because integration over several parameters may be required. This can result in lengthy computing times when decision analyses are conducted. The median can also result in lengthy computing times, since it must often be found numerically.

In contrast, the posterior mode can be computed more quickly (e.g., by nonlinear minimization). Therefore, in this paper, the baseline estimator of the quantities of interest was the posterior modal value, and management procedures were based on the posterior modal estimates. If distributions are skewed, the modal value can be considerably smaller than the expectation or median, and, depending on the estimated quantities used in the management procedure, the decision analysis results could be either less or more optimistic than if the expectation or median were used.

We conducted some evaluations to test the sensitivity of decision analysis results to using estimates based on the posterior median and also on the posterior mean. Marginal posterior distributions for model quantities were approximately lognormal. Therefore, proxies for the mean, $\bar{X}$, and median, X_{50}, for various quantities were obtained using the mode, $\hat{X}_{\text{mode}}$, estimated by nonlinear minimization and the posterior SD, $\hat{\sigma}$, estimated from the inverse Hessian matrix (Appendix 2). Mean values were approximated using

$$\bar{X} = \hat{X}_{\text{mode}} \exp(1.5\hat{\sigma}^2)$$

where $X \sim \text{lognormal}(X_{50}, \sigma^2)$. Median values, X_{50}, were approximated using

$$\hat{X}_{50} = \hat{X}_{\text{mode}} \exp(\sigma^2).$$

Results

Resource recovery and harvest rate cap decision rules

Deterministic conditions and perfect information

The deterministic relationship between catch and stock size for four different values of α in the resource recovery rules (eqs. 12 and 18) under perfect information is demonstrated in Fig. 1 for both the catch and effort control rules, i.e., the MSY quota, MSY harvest rate, and MSY effort control rules. Note that the latter two rules are deterministically equivalent and produce the exact same catch for each given

© 1998 NRC Canada

Table 1. Consequences of alternative decision rules to promote resource recovery and to reduce the risk of high harvest rates.

HR*	p	α	σ_ω	Other	$\overline{C}$	$\%P(B_y < 0.2K)$	$\%B_{fin}/K$
Effort control rules							
NA	1	0	0	PI	137	11	42
NA	1	1	0	PI	146	0.1	50
NA	1	0	0.1	—	135	29	39
NA	0.9	0	0.1	—	136	13	50
NA	0.8	0	0.1	—	130	5.5	61
NA	0.7	0	0.1	—	120	2.9	70
NA	1	0.5	0.1	—	138	18	47
NA	1	1	0.1	—	138	15	50
NA	1	2	0.1	—	138	14	53
NA	1	6	0.1	—	137	13	57
0.5	1	0	0.1	—	132	8.1	56
0.5	1	0.5	0.1	BL	132	6.3	58
0.5	1	1	0.1	—	132	4.8	59
0.5	1	6	0.1	—	131	4.8	62
0.5	1	0.5	0.0	—	134	4.5	56
0.5	1	0.5	0.2	—	126	8.6	61
0.25	1	0	0.1	—	81	2.5	80
Harvest rate control rules							
NA	1	0	0	PI	137	11	43
NA	1	1	0	PI	145	3.9	50
NA	1	0	0.1	—	126	45	38
NA	0.9	0	0.1	—	122	30	48
NA	0.8	0	0.1	—	115	18	59
NA	0.75	0	0.1	—	110	12	64
NA	0.7	0	0.1	—	105	8.5	69
NA	0.6	0	0.1	—	91	4.3	77
NA	0.5	0	0.1	—	77	1.4	83
NA	1	0.5	0.1	—	125	41	43
NA	1	1	0.1	—	125	40	46
NA	1	2	0.1	—	124	38	49
NA	1	6	0.1	—	122	37	53
NA	0.75	0.5	0.1	—	110	12	65
NA	0.75	1	0.1	—	112	11	66
NA	0.75	6	0.1	—	111	11	68
0.5	1	0	0.1	—	124	24	55
0.5	1	0.5	0.1	—	124	21	58
0.5	1	1	0.1	—	123	20	60
0.5	1	6	0.1	—	121	18	66
0.5	1	0.5	0	—	125	21	57
0.5	1	0.5	0.2	—	119	22	60
0.5	0.75	0	0.1	—	109	8.4	68
0.5	0.75	0.5	0.1	BL	109	8.0	69
0.5	0.75	6	0.1	—	108	7.6	72
0.5	0.70	0.5	0.1	—	103	5.9	73
0.5	0.65	0.5	0.1	—	98	4.6	76
0.25	1	0	0.1	—	90	2.4	76
0.25	1	0	0.1	—	90	2.1	77
0.25	0.75	1	0.1	—	89	1.9	78

© 1998 NRC Canada

Table 1 (*concluded*).

HR*	p	α	σ_ω	Other	$\bar{C}$	$\%P(B_y < 0.2K)$	$\%B_{fin}/K$
MSY quota rules							
NA	1	0	0.1	PI	133	5.1	56
NA	1	1	0.1	PI	135	0.8	61
NA	1	0	0.1	—	98	9.3	66
NA	0.9	0	0.1	—	86	2.6	75
NA	0.8	0	0.1	—	74	1.0	70
NA	1	0.5	0.1	—	98	8.4	67
NA	1	1	0.1	—	98	7.6	68
NA	1	6	0.1	—	97	7.0	70
0.5	1	0	0.1	—	98	6.6	69
0.5	1	0.5	0.1	BL	98	5.8	70
0.5	1	1	0.1	—	97	5.1	70
0.5	1	6	0.1	—	96	4.8	73
0.5	1	0.5	0	—	99	4.4	71
0.5	1	0.5	0.2	—	94	6.6	69

Note: HR* is the value for harvest rate above which there is a 0.01 probability of higher harvest rates (NA is "not applicable"), p is a policy control parameter, α is a parameter for resource recovery, σ_ω is the interannual SD in the logarithm of q, "other" refers to other information about the run (PI is the case with perfect information and BL is baseline), $\bar{C}$ is the average catch, $\%P(B_y < 0.2K)$ is the percentage probability that stock biomass falls below $0.2K$ at any time in the management horizon, and $\%B_{fin}/K$ is the stock biomass in the final year of management as a percentage of K.

level of depletion and value for α. Figure 1 demonstrates very clearly that as α increases, each management procedure becomes more conservative. Furthermore, while a value for $\alpha > 0$ results in more conservative actions for each control rule than when $\alpha = 0$, it is only with the MSY quota control rule that the replacement yield can be exceeded when $B_y < 0.5K$ (e.g., for $\alpha = 0.5$, Fig. 1*a*). For values of $\alpha > 1$, catches under the MSY quota rule were less than the replacement yield for all levels of depletion. However, recall that these results pertain only to deterministic conditions with perfect information.

Before proceeding, we will present results given when perfect information on stock size and parameter values and stochastic stock dynamics were assumed. These will serve as benchmarks to indicate the relative performance of procedures that do not have perfect information. The value assumed for p was 1 for these evaluations. The average catches for the effort control, harvest rate, and MSY quota rules were 137, 137, and 133, respectively (Table 1). Risks of stock depletion (probability of stock biomass dropping below $0.2K$, $\%P(B_y < 0.2K)$) were 11, 11, and 5.1%, respectively. Values for depletion ($\%B_{fin}/K$) were 42, 43, and 56%, respectively. When α in the resource recovery rule (eqs. 12 and 18) was set to 1, catches changed to 146, 144, and 135, respectively. Risks changed to 0.1, 3.9, and 0.8%, respectively. Thus, as expected, the effort and harvest rate control rules gave similar results under perfect information because they are deterministically identical. Performance improved with the resource recovery rule because stock dynamics were not deterministic and the resource recovery rules enabled stock recovery when stock sizes decreased below their deterministic equilibrium values. For all subsequent results, imperfect information and stochastic population dynamics were applied.

Case without harvest rate cap and resource recovery rules

The resource recovery rule was disabled by setting the policy tuning parameter α to 0. The harvest rate cap rule was disabled by setting the maximum critical harvest rate (HR*) to 1 and P^* to 1. When the harvest control fraction, p, was set to 1, the effort control and MSY harvest rate policies yielded slightly lower average catches (135 and 126, respectively) but much higher risks (29 and 45%, respectively) than the case with perfect information (Table 1). Expected depletion was 39 and 38%, respectively. In contrast, the MSY quota rule yielded much lower values for average catch (98) and higher values for risk and depletion (9.3 and 66%, respectively) than the case with perfect information. For the effort control and harvest rate policies, p had to be reduced to 0.8 and 0.6, respectively, before the risk dropped to a relatively low value (5.5 and 4.3%, respectively) (Table 1). Depletion increased to 61 and 77%, respectively, and average catches dropped by 3 and 28%, respectively.

Case with harvest rate cap and resource recovery rules

When the resource recovery rules were applied to the effort and harvest rate control rules with p set at 1, risks dropped for both policies but still remained relatively high. For the effort control rule, risk dropped from 29 to 18 and 13%, respectively, when α was increased from 0 to 0.5 and 6, respectively (Table 1). Depletion increased to 47 and 57%, respectively, and average catch increased to 138 and 137, respectively. For the harvest rate control rule, risk dropped from 46 to 41 and 37% when α was increased from 0 to 0.5 and 6, respectively. Depletion increased to 43 and 53%, respectively, and average catch decreased to 125 and 122, respectively. When p was set at 0.75 and α was changed from 0 to 0.5 and 6 for the harvest rate control rule, the risk changed very little (from 12 to 12 and 11%, respec-

© 1998 NRC Canada

tively). Average catch changed very little (110 and 109, respectively). Depletion increased slightly from 64 to 65 and 68%, respectively. The resource recovery rule had relatively little effect on performance indices of the MSY quota control rule, partly because risks were already small (Table 1). For example, average catch remained the same at 98 but risk dropped from 9.3 to 7.0% when α was changed from 0 to 6.

When the harvest rate cap rules were applied to the effort and harvest rate control rules with p and α set at 1 and 0, respectively, risks dropped for both management procedures but still remained relatively high for the latter. In all cases where the harvest rate cap rules were applied, P^* was set at 0.01. For the effort control rule, risk dropped from 29 to 8.1 and 2.5% when HR* was set to 0.5 and 0.25, respectively (Table 1). Depletion increased to 56 and 80%, respectively, and average catch changed to 132 and 81, respectively. For the harvest rate control rule, risk dropped from 45 to 24 and 2.4% when HR* was set to 0.5 and 0.25, respectively. Depletion increased to 55 and 76%, respectively, and average catch changed to 124 and 90, respectively. When p was set at 0.75 and when HR* was set to 0.5 and 0.25 for the harvest rate control rule, the risk dropped from 12 to 8.4 and 1.9%, respectively. Average catch dropped slightly from 110 to 109 and 89, respectively, and depletion increased slightly from 64 to 67 and 78%, respectively. The harvest rate cap rule also had relatively little effect on performance indices of the MSY quota control rule, also because risks were already small (Table 1). For example, average catch remained the same at 98, but risk dropped from 9.3 to 6.6% when HR* was set to 0.5.

The joint implementation of the resource recovery and harvest rate cap rules allowed higher harvest rates at larger stock sizes and slight increases in average catch for fixed levels of risk. For the effort control rule, when HR* was changed from 1 to 0.5 and α was changed from 0 to 0.5, catch decreased from 135 to 132, risk decreased from 29 to 6.3%, and depletion increased from 39 to 58% (Table 1). An effort control rule without the harvest rate cap and resource recovery rules that had a similar level of risk (i.e., with p = 0.8 and a risk of 5.5%) had an average catch of 130. For the harvest rate control rule, when p was set at 1, HR* was changed from 1 to 0.5, and α was increased from 0 to higher values, risks remained high, e.g., with α = 6, risk was 18%. When p was set at 0.75, HR* was changed from 1 to 0.5, and α was increased from 0 to higher values, risks dropped below 0.1, e.g., with α = 0.5, risk decreased from 12 to 8.0%. Catch decreased slightly from 110 to 109 and depletion increased slightly from 64 to 69% (Table 1). A harvest rate policy without the harvest rate cap and resource recovery rules that had a similar level of risk (i.e., with p = 0.7 and a risk of 8.5%) had an average catch of 105. Policy performance for the MSY quota rule changed very slightly with the introduction of both rules. For example, risk, average catch, and depletion changed from 9.3, 98, and 66 to 5.8, 98, and 70% when p was set at 1 and α and HR* were changed from 0 and 1 to 0.5 and 0.5, respectively (Table 1).

Thus, the performance of the effort control rule was enhanced by the harvest rate cap and resource recovery rules much more so than was that of the harvest rate and MSY quota rules. As mentioned before, the MSY quota control rule was less sensitive to these rules mainly because risks were already low. The harvest rate rule was less sensitive because the harvest control function for the harvest rate control rule was less precisely estimated than that for the effort control rule (see below). Furthermore, for each of the harvest control rules, slight increases in average catch can be obtained for a fixed level of risk by implementing the harvest cap and resource recovery rules, particularly the former.

The baseline values for α, HR*, and P^* were set at 0.5, 0.5, and 0.01, respectively. Note that for the MSY quota rule under deterministic conditions, a value of $\alpha < 1$ can result in catches larger than the replacement yield at stock sizes less than $0.5K$ (Fig. 1). However, as risks were already relatively low for this rule, and values of $\alpha > 0$ stimulated precautionary action, the use of α = 0.5 resulted in even lower risks. The baseline values, by our experience, would give intermediate estimates of risk that were on the threshold of acceptability for fishery managers. Thereby, the effects of further sensitivity tests could be revealed most readily by pushing risk estimates in either direction (e.g., if a risk estimate is already very low, then a change making it lower would not be as revealing as a baseline case with an intermediate level of risk).

Evaluating catch control versus effort control rules

Of the three families of management procedures evaluated, the effort control rules gave the highest average catch for a given level of risk and the lowest interannual variability in effort. For example, with p = 1 and α = 1, risk was 4.8% and the average catch was 132, nearly 40% larger than values given by the harvest rate and MSY quota control rules with similar levels of risk (see below and Table 1). The average annual change in effort was 10, 24, and 20% for the MSY effort, MSY harvest rate, and MSY quota policies, respectively. Furthermore, unlike the other two harvest control rules in which reasonably low risks could only be obtained by underexploiting the stock ($E(B_{fin}) \geq 0.7K$), the effort control rules with low risks (e.g., 6.3%) depleted the stock to levels slightly higher than that at MSY (e.g., $0.58K$) (Table 1). However, under effort control, the average interannual change in catch was at least as high as it was for the harvest rate rule and larger than that for the MSY quota rule (e.g., with p = 1 and α = 0.5, the values were 18, 18, and 11% for the effort, harvest rate, and MSY quota rules, respectively) (Table 2).

The harvest rate control rule with p = 1 and α = 0.5 resulted in lower average catches and higher risks and interannual variability in effort than the effort control rules and higher interannual variability in catch than the MSY quota rules. For example, for the harvest rate rule, risk was 21%, the average catch was 124, and the average relative interannual change in effort was 24% (Table 2). A harvest rate rule with p = 0.75 reduced risk to 8.0%. However, interannual variability in effort (22%) remained high compared with that for the effort control rule (10%). Furthermore, the stock was on average left at a relatively underexploited state ($0.69K$). The expected average catches for harvest rate rules were considerably less than those for the effort control rules with comparable levels of risk. For example, under effort control with p = 1, α = 1, and HR* = 0.5, risk was 4.8% and average catch was 132. Under a harvest rate control rule

© 1998 NRC Canada

Table 2. Consequences of alternative catch control and effort control rules.

Control rule	p	$\bar{C}$	$\%\Delta C$	$\%\Delta E$	$\%B_{fin}/K$	$\%P(B_y < 0.2K)$
Effort	1	132	18	10	58	6.3
Harvest rate	1	124	18	24	58	21
Harvest rate	0.75	109	14	22	69	8.0
MSY quota	1	98	11	20	70	5.8

Note: $\%\Delta C$ is the average percent annual change in catch and $\%\Delta E$ is the percent annual change in effort. α and HR* were both set at 0.5.

Table 3. Policy consequences under alternative hypotheses for r.

Control rule	Indicator	$r < 0.25$	$0.25 < r < 0.5$	$0.5 < r < 0.75$	$r > 0.75$	$E(X)$
Harvest rate	%EMAE(TAC)	62	37	43	56	44
	%Bias(TAC)	40	−11	−35	−54	−13
	%Bias(r)	72	10	−23	−42	7.3
	%Bias(B_y)	−15	−8.3	0.4	4.3	−6.2
	$\%B_{fin}/K$	45	55	63	83	58
	$\bar{C}$	80	113	152	183	124
	$\%P(B_y < 0.2K)$	34	20	17	13	21
Effort	%EMAE(E_{MSY})	48	27	26	33	31
	%Bias(E_{MSY})	32	1	−17	−29	−0.9
	%Bias(r)	65	6.8	−25	−42	4
	%Bias(q)	41	15	−2	−10	13
	$\%B_{fin}/K$	51	55	61	78	58
	$\bar{C}$	82	119	164	204	132
	$\%P(B_y < 0.2K)$	13	7.2	2.2	0	6.3
MSY quota	%EMAE(TAC)	51	29	36	47	36
	%Bias(TAC)	30	−12	−31	−45	−13
	%Bias(r)	68	−1.7	−35	−53	−3.3
	%Bias(K)	−25	−8.6	7.8	19	−4.8
	$\%B_{fin}/K$	55	68	76	87	70
	$\bar{C}$	70	92	115	132	98
	$P(B_y < 0.2K)$	11	5.8	3.2	2.6	5.8

Note: The averages were taken over the 30-year management period. %EMAE(X) is the expected mean absolute percent error in the estimated quantity X (e.g., TAC or total allowable catch), %Bias(X) is the average percent bias in the estimated quantity X, and $E(X)$ is the expected value of quantity X averaged across all hypotheses. p was 1 for each harvest control rule, and α and HR* were both set at 0.5.

($p = 0.65$ and $\alpha = 0.5$) with a similar risk (4.6%), average catch was only 98 (Table 1).

The harvest rate control rules yielded lower average catches, at comparable levels of risk, than the effort control rules for several different reasons. Firstly, the TAC in a harvest rate control rule is estimated much less precisely than the effort at MSY. For example, for the harvest rate control rule with $p = 1$, the %EMAE in the estimated TAC averaged across years was 44% (Table 3). In contrast, the %EMAE in the estimated effort at MSY was 31%. (Note that the %EMAE reflects both bias and imprecision and thus is only an approximate index of imprecision.) The TAC is imprecisely estimated because it is a product of the estimate of $r/2$ and stock biomass, which are both imprecisely estimated, especially in the first few years of management, and are not strongly correlated. In contrast, effort at MSY is the quotient $r/2q$, and estimates of r and q tend to be positively correlated. This leads to reduced variance in estimates of effort at MSY.

Secondly, estimates of the TAC tend to be positively biased when the actual values of either K or r are low. For example, when $r < 0.25$, the TAC was on average 40% too large (Fig. 2*b*; Table 3). This was partly because the estimate of r tended to have a strong positive bias (72%, averaged over years) when $r < 0.25$ (Table 3). The estimates of biomass when $r < 0.25$ had a negative bias, but this bias (−15%) was much smaller in magnitude than the positive bias in r. The resulting overestimates of TAC (by 40%) when r was low tended to increase the risk of stock depletion. In contrast, under the effort control rule, the estimates of r and q both had strong positive biases when $r < 0.25$ (i.e., 65 and 44%, respectively). Therefore, the estimate of effort at MSY for $r < 0.25$ had a smaller average bias (i.e., 32%) than the estimated TAC under the harvest rate control rule (Fig. 2*b*).

Thirdly, the rate of learning over time was higher for the effort control rule than for the harvest rate control rule. For example, after 30 years of effort control, %EMAE in the target effort level was 19% (Fig. 2*a*). In contrast, the %EMAE in estimates of the TAC was 36% under the harvest rate control rule. Thus, even after 30 years of management, the harvest rate control rule was more prone to large errors in

© 1998 NRC Canada

Fig. 2. (*a*) Expected mean absolute percent error in the estimated target management quantity for the baseline MSY quota, effort control, and harvest rate control management procedures with $p = 1$, HR* = 0.5, and $\alpha = 0.5$; (*b*) expected percent bias in the target effort and the target TAC for these three management procedures when $r < 0.25$. Note that management begins in year 21.

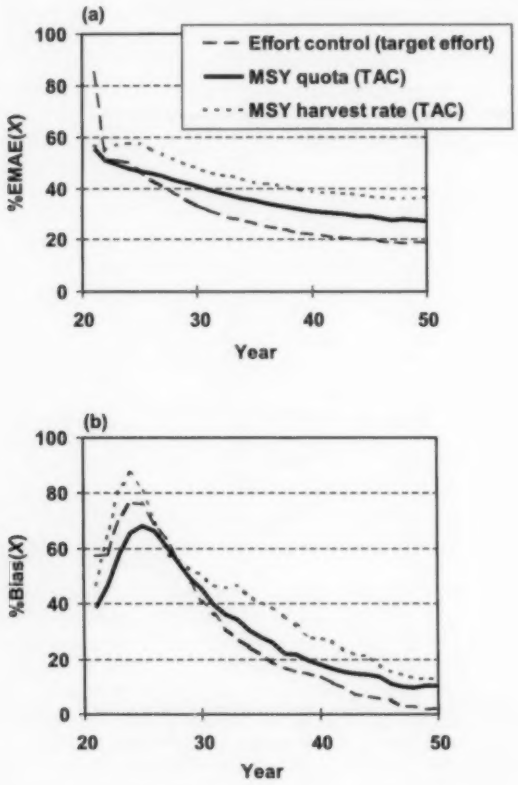
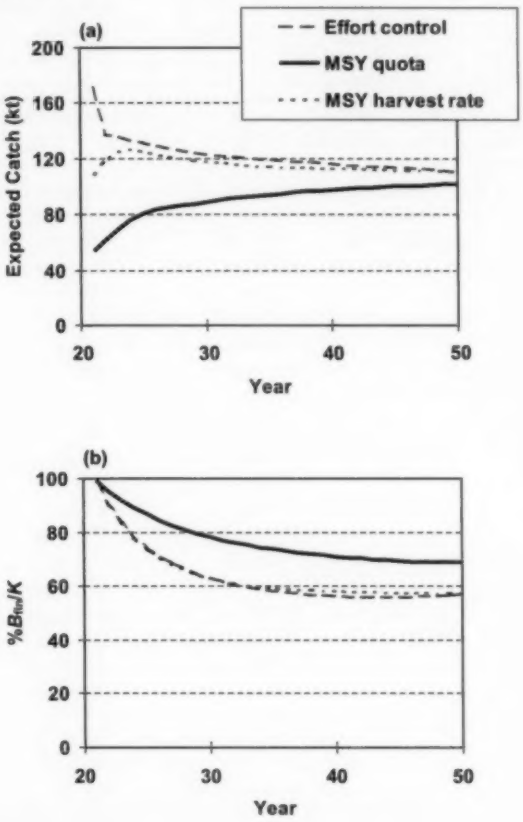


Fig. 3. Expected (*a*) catches and (*b*) depletion under the baseline effort control, harvest rate, and MSY quota management procedures.



estimates of the harvest control variable, i.e., the TAC, and to causing overharvesting than the effort control rule.

The MSY quota rules resulted in much lower average catches for the same level of risk than effort control rules. For example, with $p = 6$, risk was 4.8% and the average catch was 96 (Table 1). In contrast, for an effort control rule with similar risk (4.8%), catch was 132. The MSY quota rule also left the stock at a relatively underexploited state (e.g., under the baseline MSY quota management procedure, depletion was 69%) compared with the harvest rate and effort procedures (55 and 58%, respectively). The MSY quota rule, however, tended to produce average catches similar to the harvest rate rule for the same level of risk (Table 1).

The MSY quota rule yielded lower average catches for levels of risk comparable with the effort control rule for a few different reasons. Firstly, the MSY quota rule, by design, generated a much slower rate of fishing down than the effort control rule, since the expected yields during fishing down were more or less equal to the long-term MSY (Fig. 3). In contrast, under the effort control rule, the yields during fishing down are expected to be given by the effort (or, roughly, harvest rate) at MSY, and yields will be larger when biomass is larger (Fig. 3). Therefore, average catches are expected to be lower for the MSY quota than for the effort control rule.

When r was low (e.g., $r < 0.25$), estimation performance was slightly better for the effort control rule than for the MSY quota rule. For example, the expected trajectories of bias in the estimates of the TAC under the effort control rule approached 3% after 30 years. In contrast, bias in the estimate of the TAC appeared to asymptote at about 11% (Fig. 2*b*). The estimation properties for effort at MSY and MSY are not dissimilar because of the covariance between the model parameters that underlie these quantities (i.e., r and q and r and K, respectively). As mentioned earlier, the positive posterior covariance between estimates of r and q tended to dampen bias and variance in the estimate of the effort at MSY. Similarly, the negative posterior covariance between estimates of r and K also tended to dampen the bias and variance in the estimate of MSY ($rK/4$). However, the lower catches under the MSY quota rule tended to generate lower contrasts in the catch rate data than the effort control rule, and this decreased estimation performance. For example, after 30 years of exploitation the %EMAE in estimates of the TAC (27%) was larger than that in the target effort level (19%) under the MSY effort procedure (Fig. 2*a*). Thus,

© 1998 NRC Canada

Table 4. Consequences of various biases in prior medians under the baseline procedure (i.e., the effort control rule with α and HR* both set at 0.5).

Source of bias	$\bar{C}$	$\%B_{final}/K$	$\%P(B_y < 0.2K)$
Baseline	132	58	6.3
$q_{50} = 0.05$	138	55	17
$q_{50} = 0.2$	117	62	1.9
$K_{50} = 2000$	137	55	9.9
$K_{50} = 500$	121	63	3.3
$r_{50} = 0.8$	115	68	3.4
$r_{50} = 0.2$	117	62	1.9

Note: The unbiased medians for the priors were $q_{50} = 0.1$, $r_{50} = 0.4$, and $K_{50} = 1000$.

the combination of lower average catches and slightly poorer estimation performance for the MSY quota resulted in slightly lower risks when r was low (Table 3).

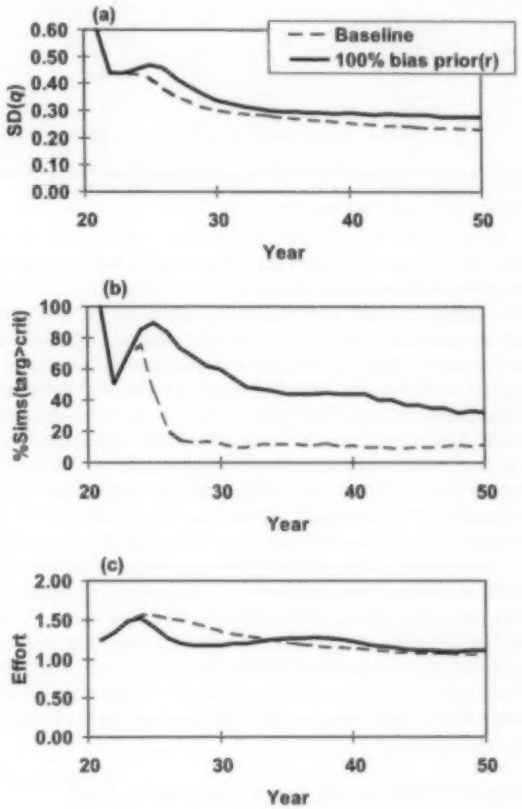
We also evaluated the sensitivity of policy performance to different values for the SD for interannual variability in q, σ_ω. The baseline value for σ_ω was 0.1. The performance of the effort control rule was more sensitive to changes in this parameter than that of the other two control rules. When σ_ω was decreased to 0, average catch for the effort control rule increased from 132 to 134 and risk decreased slightly from 6.3 to 4.5% (Table 1). Under the MSY quota and harvest rate rules, average catches increased by one unit each. Risks decreased slightly from 5.8 to 4.4% for the MSY quota rule, but remained the same for the harvest rate rule. When σ_ω was set to 0.2, average catch for the effort control policy decreased to 126 and risk increased to 8.6%. In contrast, under the MSY quota and harvest rate rules, average catch changed only slightly to 94 and 119, respectively, and risk to 6.6, and 22%, respectively. However, even with large variability in q, the effort control rule yielded larger average catches for the same level of risk than the catch control rules.

The baseline procedure that was used in subsequent evaluations was the effort control rule with values for p, α, HR*, and P^* set at 1.0, 0.5, 0.5, and 0.01, respectively.

Effects of biased priors

Twofold biases in the medians of some of the stock assessment priors increased risks considerably over baseline values. For example, when a 50% negative bias was introduced in the median of the stock assessment prior for q (i.e., the median for q was decreased from the true value of 0.1 to 0.05), the risk of stock depletion increased to 17% (Table 4). The effect of having a positively biased stock assessment prior for K was less pronounced. For example, the risk of stock depletion was only 9.9%. Curiously, the effect of a 100% positive bias in the prior for r was to reduce the risk from 6.3 to 3.4%. Average catches were 11% less under this scenario than the baseline. Risks and average catches were lower because the posterior SDs in the stock assessment estimates of q dropped more slowly with the positively biased prior for r and reduced the maximum cap on effort more so than the baseline case (Fig. 4). Therefore, the maximum cap was met more often and lower effort and catch levels were implemented than in the baseline case, especially when r was low (e.g., <0.25).

Fig. 4. (*a*) Posterior SDs in estimates of q, (*b*) percentage of simulations in which estimates of the target effort exceeded the critical effort level, and (*c*) effort for the baseline effort control management procedure with unbiased priors and a case with the median for the prior for r biased by 100%. True simulated values for r are <0.25.



Negatively biased priors for r and K and a positively biased prior for q lowered risks and catches (e.g., catches decreased by 8% with a –50% bias in the prior for K and by 11% for a 100% bias in the prior for q) (Table 4).

Effects of higher versus lower prior and posterior precision

In the first set of trials, the prior and posterior distributions in the stock assessment and decision analysis, respectively, were made more precise and then less precise than in the baseline case. Risks tended to decrease with decreasing precision. For example, when the probability distributions for K were less precise (i.e., the CV increased from 0.6 to 0.8), the risk of stock depletion decreased slightly to 4.4% and the average catch increased to 143. This increase in catch resulted because the mean of the posterior distribution for K increased with the increase in the posterior variance (the median was kept the same). Risks changed very little because, among other things, higher prior CVs caused the harvest rate cap rule to lower the harvest rate caps. When the CVs for r were increased from 0.5 to 0.7, risk and the expected average catch decreased to 4.4% and 123, respec-

© 1998 NRC Canada

Table 5. Consequences of using precise versus imprecise posteriors and priors in decision analysis and stock assessment, respectively.

Parameter	Prior CV	$\bar{C}$	$\%B_{fin}/K$	$\%P(B_y < 0.2K)$
Baseline (K, r, q)	0.6, 0.5, 0.6	132	58	6.3
K	0.8	143	60	4.4
K	0.4	123	55	6.6
r	0.7	122	63	4.4
r	0.3	133	50	8.3
q	0.8	123	59	3.6
q	0.4	139	55	7.8

Note: Results were calculated using the baseline effort control rules, and α and HR* were both set at 0.5

Table 6. Consequences of using precise versus imprecise priors in stock assessment only.

Parameter	Prior CV	$\bar{C}$	$\%B_{fin}/K$	$\%P(B_y < 0.2K)$
Baseline (K, r, q)	0.6, 0.5, 0.6	132	58	6.3
K	0.8	130	59	4.9
K	0.4	132	56	6.4
r	0.7	123	63	3.3
r	0.3	137	50	10
q	0.8	124	59	3.5
q	0.4	135	56	10

Note: Results were calculated using the baseline effort control rules, and α and HR* were both set at 0.5.

tively. The effects were similar when the CVs for q were increased from 0.6 to 0.8 (Table 5).

In contrast, when the CVs in the decision analysis and stock assessment were decreased, the risk of overexploitation increased slightly. For example, when the CVs for K were lowered from 0.6 to 0.4, the risk increased to 6.6% and average catch decreased to 123 (Table 5). Average catch decreased partly because the mean of the marginal posterior for K in the decision analysis decreased with a decrease in the posterior CV. Risk increased slightly despite the lower catches partly because with added prior precision in K in the stock assessments, it took longer to learn that K and B_y were low when they were actually low. Larger catches and marked depletion occurred before assessments homed in on the correct value for K. These effects are illustrated in more detail in the next section. For similar reasons, the risks of implementing more precise priors for r and q increased also (to 8.3 and 7.8%, respectively) (Table 5). However, average catches were larger than in the baseline case (i.e., 133 and 139, respectively).

Effects of higher versus lower precision in stock assessment priors only

When precision was modified in the stock assessment priors only, the effects of increased versus decreased precision were more pronounced. The posterior CVs that were used in the decision analysis were held constant at the baseline values of 0.6, 0.5, and 0.6 for K, r, and q, respectively. When the prior CV for q, r, and K in the stock assessments was increased to 0.8, 0.7, and 0.8, respectively, the risks decreased to 4.9, 3.3, and 3.5%, respectively (Table 6). When the prior CVs for q, r, and K in the stock assessments were decreased to 0.4, 0.3, and 0.4, respectively, the risks increased to 10, 10, and 6.4%, respectively.

The effects of using overly precise priors can be illustrated by examining the decision analysis results for low versus high values of r. The expected consequences of the baseline harvest procedure were calculated under four alternative hypotheses for r: (*i*) $r \leq 0.25$, (*ii*) $0.25 < r \leq 0.50$, (*iii*) $0.50 < r \leq 0.75$, and (*iv*) $r > 0.75$. If we consider the results for the situation in which the prior CV for r in the stock assessment is set to 0.7, risks of stock depletion remain relatively low under each of the hypotheses for r (Table 7). In contrast, when the prior CV for r was set at 0.3, the risks were relatively high for all but the most optimistic hypotheses for r. Average catches increased as the hypotheses for r became less pessimistic, and average catches were larger under each of the hypotheses than when the prior for r was less precise. This resulted for a few different reasons. Firstly, estimated target effort is based on the modal estimate of r and q. The mode of a lognormal distribution is given by

$$X_{mode} = X_{50} \exp(-\sigma^2)$$

where X_{50} is the median value of X and σ is the lognormal SD. Clearly, the smaller the value for σ, the larger the value for the mode. For example, when the prior CV for r was 0.3, the prior mode for r was 0.365. When the prior CV for r was 0.7, the prior mode for r was 0.245. Therefore, when the CV in r was set to 0.3 rather than to 0.7, the initial target effort levels were 33% larger.

The main effect of overestimating r when r was small was to cause an overestimate of the target MSY effort level, especially in the first few years of harvest. For example, when the true value for r was less than 0.25, the target effort level was overestimated by 259 and 140% in the first year for the cases with a prior CV on r of 0.3 and 0.7, respectively (Table 7).

When the prior CV for r was lowered to 0.3, effort levels were higher and the upper cap for effort was approached more often in the first few years of management (Fig. 5). However, when the CV in r was raised to 0.7, after the first few years, the cap for effort was met much more frequently. This is partly because the posterior SD in q decreased more rapidly when the prior CV in r was small and thereby yielded higher values for the effort cap than when the prior CV in r was larger (Fig. 5). Consequently, when the prior CV for r was small, effort levels were on average higher under all hypotheses for r (Fig. 5).

Finally, the precise prior for r decreased the ability for the stock assessment to home in on the true value if the true value happened to be much lower or higher than the value at the mode of the prior. For example, with a prior CV of 0.7, and actual values for r were less than 0.25, the average bias in the estimate of r in the final year was 44% too large (Table 7). In contrast, when the prior CV for r was 0.3, this bias was 59% too large. When the actual value for r was greater than 0.75, the respective biases were –24 and –33% for the cases with prior CVs for r of 0.7 and 0.3, respectively.

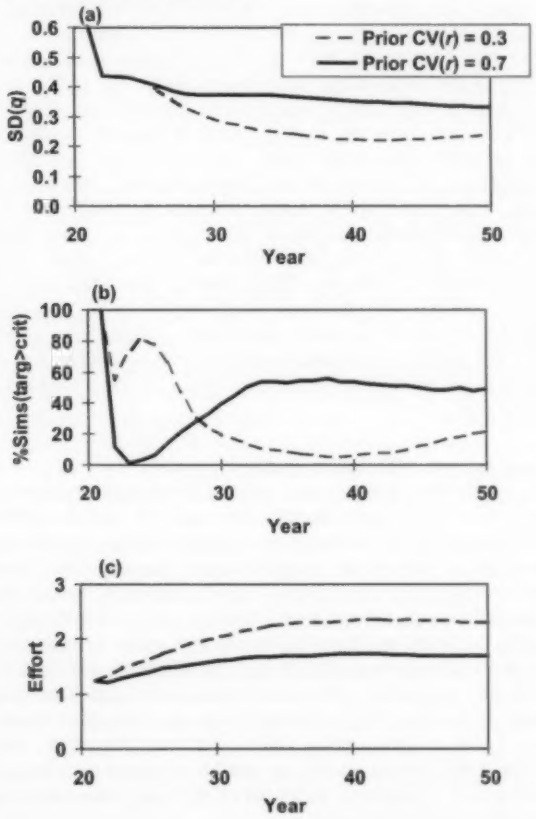
© 1998 NRC Canada

Table 7. Consequences of using a precise versus imprecise prior for r under alternative hypotheses for r.

Prior CV(r)	Indicator	$r < 0.25$	$0.25 < r < 0.5$	$0.5 < r < 0.75$	$r > 0.75$	$E(X)$
0.7	$\%P(B_y < 0.2K)$	8.0	3.1	1.6	0	3.3
0.7	$\overline{C}$	80	114	151	177	124
0.7	$\%\text{Bias}(E_{MSY})$ yr 1	140	19	−29	−56	20
0.7	$\%\text{Bias}(r)$ yr fin	44	20	−8	−24	−13
0.3	$\%P(B_y < 0.2K)$	16	11	6.0	2.6	10
0.3	$\overline{C}$	84	121	172	227	137
0.3	$\%\text{Bias}(E_{MSY})$ yr 1	259	77	6	−35	78
0.3	$\%\text{Bias}(r)$ yr fin	59	21	−12	−33	14

Note: $\%\text{Bias}(X)$ yr 1 is the percent bias in quantity X in the first year of management, and $\%\text{Bias}(X)$ yr fin refers to the percent bias in quantity X in the final year of management. Results were calculated using the baseline effort control rules, and α and HR* were both set at 0.5.

Fig. 5. (*a*) Posterior SDs in estimates of q, (*b*) percentage of simulations in which estimates of the target effort exceeded the critical effort level, and (*c*) effort for cases with the prior CV(r) = 0.7 and the prior CV(r) = 0.3 under the baseline effort control management procedure.



Effects of using the posterior median and means as estimators

When the posterior median and mean were used as estimators for the harvesting decision rules, average catches and the risks of stock depletion increased considerably for the MSY harvest rate and MSY quota control rules. For example, for the median estimator, average catch increased by 15 and 29%, respectively, and risk increased to 22 and 34%, respectively (Table 8). However, for the effort control rule, the average catch and risk changed very little. Catches were both 132 and the risk was 8.6 and 9.3% for the median and the mean estimators, respectively. The differences in performance resulted mainly from the position of the estimated quantities in the harvest function decision rules. In the MSY harvest rate and MSY quota policies, the estimated quantities were all products of each other. Because the median and mean estimators were larger in value than the mode estimator, the products of the former estimators would result in larger catch quotas and larger risks. However, for the MSY effort procedure, the two estimated quantities, r and q, were split between the numerator and the denominator. Therefore, when the effort at MSY was calculated, the higher estimates of r and q effectively canceled. Further tests indicated that the effects on management performance from using different prior CVs were relatively insensitive to whether the posterior mean, median, or mode was used as the estimator.

Discussion

In this paper, we presented a Bayesian decision analytic procedure that could be applied in developing fisheries. We applied the approach to a hypothetical situation to evaluate the potential consequences of catch control versus effort control rules when a biomass dynamic model is fitted to catch rate data. As expected, the weaker probing policies, such as those given by the MSY quota rules, generally provided lower average catches and lower risks than the stronger probing policies, such as those given by the effort control and harvest rate control rules. This was because the MSY quota option applied a more or less constant target quota and tended to result in lower harvest rates in the initial years. In contrast, the stronger probing policies were both, in effect, harvest rate strategies that took a more or less fixed fraction of biomass from the stock each year and could result in high harvest rates even in the first few years of management.

The most astonishing result was the marked superiority of the effort control management options over the catch control options. While the effort control and harvest rate control options were deterministically equivalent, the effort control option provided average catches up to 40% larger at similar risks of stock depletion. This superiority in performance

© 1998 NRC Canada

Table 8. Consequences of alternative management procedures using different estimators.

Control rule	p	Estimator	$\bar{C}$	$\%B_{fin}/K$	$\%P(B_y < 0.2K)$
Effort	1.0	Mode (baseline)	132	58	6.3
		Median	132	57	8.6
		Mean	132	56	9.3
Harvest rate	0.75	Mode (baseline)	109	69	8.0
		Median	125	61	22
		Mean	126	59	27
MSY quota	1.0	Mode (baseline)	98	70	5.8
		Median	124	55	29
		Mean	126	53	34

Note: Results were calculated using the baseline effort control rules, and α and HR* were both set at 0.5.

given by effort control mainly resulted from the smaller variance and bias in estimates of the effort targets than in the catch control targets in the harvest rate and MSY quota control options.

The evaluations in our paper suggest that the implementation of quantitative decision rules to reduce the risk of high harvest rates and to promote resource recovery when stock size is depleted can improve policy performance considerably. Larger average catches can be obtained for the same levels of risk and higher harvest rates can be implemented when stock size is large (e.g., $B_y > 0.5K$).

Assumptions and limitations of findings

While there may be many situations in which harvesting control regimes may fail (Walters and Maguire 1996), this study indicates that harvest control management procedures could perform reasonably well under some conditions. These include the following: (1) management authorities can control the (*a*) addition of up to 25% of the fishing effort, e.g., vessels, to the fishery in years when the fishery needs to be expanded and (*b*) removal of up to 25% of the fishing effort from the fishery in years when effort needs to be reduced, (2) management authorities can obtain reasonably reliable data on catch biomass removed and total fishing effort each year, (3) management authorities obtain at least one unbiased relative index of abundance with a CV of no more than about 0.2, (4) the stock assessment procedures applied model the dynamics of the resource reasonably well and are relatively robust to uncertainty, and (5) precautionary measures, such as the ones applied in this paper, are implemented to reduce the risks of high harvest rates and achieve resource recovery if the stock becomes heavily depleted.

As mentioned before, many of the most valuable species in developing fisheries are deepwater species. Many of these species appear to be long-lived, slow-growing species (e.g., alfonsino, toothfish, and orange roughy). These species could be represented by values of r less than 0.2. In contrast, the baseline posterior distribution for r in our decision analysis had a median of 0.4. The mean results thus would appear to apply to species that are not as long lived and slow growing. An indication of potential policy performance for long-lived, slow-growing species is given in Table 3 under the column for $r < 0.2$. Under these circumstances, it appears that the effort control management option is still best. For example, for a similar average catch, 82 and 80, respectively, the catch control option has a much lower risk (13%) than the harvest rate option (34%). For a similar risk, 13 and 11%, respectively, the effort control option has a larger average catch (82) than the MSY quota option (70). However, these results pertain to a situation in which the stock assessment prior for r had a strong positive bias, and much better management performance could be expected for such deepwater species if a less biased prior for r were applied.

One of the assumptions in this paper was that catchability is constant over time and stock size. For a variety of reasons, this assumption may not hold (Walters and Maguire 1996). Some preliminary evaluations show that policy performance is considerably worse when this assumption about catchability is relaxed. Further work is needed to identify management procedures that are robust to systematic changes in catchability. In this paper, the only data used in stock assessments were catch biomass and CPUE data. Fishery-independent indices of abundance (e.g., from trawl or acoustic surveys) are often obtained for only highly valuable commercial fisheries. These indices are often used as relative indices of abundance and sometimes as absolute abundance indices. If such abundance indices were available, the catch control rules would be robust to the form of the relationship between catch and effort; effort control rules would not.

Comparisons with other studies

Several other authors have evaluated management procedures for developing fisheries. For example, Smith (1993) used Monte Carlo simulation to evaluate management procedures for a developing orange roughy resource. He found that intermediate harvest rates struck the most favourable balance between the risks of overexploitation before sufficiently accurate estimates of stock size could be obtained and chronic underexploitation because of underestimation of stock size caused by a lack of contrast in the data. The evaluation in Smith (1993) differed from ours because it evaluated catch control rules only, was non-Bayesian, and assumed that all parameters except for virgin stock size and the constant of proportionality for relative abundance indices were known without error.

In contrast, Clark et al. (1985) applied a Bayesian decision analytic approach and analytical methods to identify some optimal fishing capacity decisions for developing fisheries. They found that reasonably good decisions could be made based on relatively limited prior information about recruitment and a conservative approach to allowing increases in fishing effort. However, they considered uncertainty only for the estimate of mean recruitment, and uncertainty in the

© 1998 NRC Canada

estimates of annual recruits was ignored (i.e., there was no observation error).

The management procedures considered in this paper bear some similarity with the catch limit algorithm, developed originally by Dr. Justin Cooke, that lies at the core of the revised management procedure (RMP) of the International Whaling Commission (IWC 1994). In this algorithm, the dynamics of the whale stock are described by a modified logistic model, and Bayes-like methods are used to estimate the key parameters and determine numerical catch limits, with prior probability distributions being assigned to selected parameters. These prior distributions, however, are not standard Bayesian priors that are designed to reflect prior beliefs about the likely distribution of the corresponding biological parameters, as is the case in this paper. Rather, these "priors" were selected to provide optimum performance on designated simulation trials. Several of the other management procedures considered during the development of the RMP were also designed to be deliberately precautionary, particularly the target adjusting procedure developed by Dr. William de la Mare (IWC 1992, pp. 100–103); however, none of these incorporated any form of Bayesian analysis.

Frederick and Peterman (1995) developed a decision analytic approach to deciding how harvesting policy target quantities should be adjusted depending on the uncertainties in age-structured stock assessments. They used Monte Carlo simulation to find the adjustment to the annual allowable catch (relative to the deterministic MSY) that maximized the expected present value of the resource. Our approach differs because our uncertainty adjustment is not fixed over time but is instead dynamic. Our approach uses the estimated posterior distribution for model input parameters in each year to make an adjustment to the target harvest control to provide an acceptably low risk of a high harvest rate. The degree of precautionary action is thus a function of the uncertainty in each annual stock assessment. As uncertainty decreases, larger harvest rates may be allowed, all other things being equal. Furthermore, we did not try to optimize as they did, but simply compared the potential performance of a wide variety of alternative management procedures over a variety of performance indices. And in contrast with the use of the expected present value to identify the optimal adjustment (Frederick and Peterman 1995), our method requires the decision maker to identify the decision rule settings that result in the most favourable trade-off between decreased risks of stock collapse and decreased average catches. Our evaluations show that by implementing these decision rules, considerably lower risks of stock depletion can be obtained with very little reduction in average catch.

In their discussion of the management of northern cod, Walters and Maguire (1996) suggested a quantitative decision rule analogous to our harvest rate cap rule. They suggested that for a risk averse harvest rate strategy, in which TAC = $HR^T B_y$, the target harvest rate, HR^T, should be adjusted down by dividing by a factor of $\exp(0.5V^2)$, where V is the coefficient of variation of the stock size estimate (analogous to σ_{B_y}, the SD in the estimate of the logarithm of stock biomass, used in our paper). They also suggested that this would result in no more than a 20% chance each year of having the actual harvest rate, HR, exceed HR^T. A formal derivation of this result and simulation evaluation of its potential performance as a harvest control rule are not provided. However, our derivation above (eq. 11) suggests that if estimates of stock biomass are approximately lognormally distributed and we would like $P(HR > HR^T) \leq 0.2$, then a more appropriate formulation would be to set the TAC equal to $HR^T \mu_B \exp(-0.85\ \sigma_{B_y})$, where μ_B is the posterior median estimate of stock biomass. Moreover, it appears that Walters and Maguire's (1996) formulation would to fail to achieve their precautionary goal. For example, if σ_{B_y} were 0.5, their formula would suggest that HR^T should be multiplied by a factor of 0.88 and there would be a 40% rather than a 20% chance that annual harvest rates would exceed HR^T. In contrast, with our formulation, this factor would instead be 0.65 and the chance of exceeding HR^T would be 20%, as intended.

A commonly applied Bayesian estimator is the posterior mean (Berger 1985; Cordue and Francis 1994). Our evaluations indicate that the performance of effort control rules was relatively insensitive to whether the posterior mean, median, or mode was used as the estimator. However, the catch control rules resulted in high risks of stock depletion when the median was used and even higher risks when the mean was used as the estimator. Cordue and Francis (1994) evaluated the estimation performance of some Bayesian and non-Bayesian estimators that could be used in decision analyses of management procedures for developing fisheries. Of the Bayesian estimators evaluated, only posterior mean estimators were considered. When data were relatively uninformative, they found that a noninformative prior for q (uniform on log q) resulted in higher risks of stock depletion than a prior that favoured smaller stock sizes (uniform on q). Presumably, the posterior modal estimators considered in this paper together with the informative priors and decision rules to minimize the risk of high harvest rates would have even lower risks of stock depletion than the Bayesian estimators considered in Cordue and Francis (1994).

Recommendations about using prior distributions in stock assessment

Our evaluations corroborate recent concerns (McAllister et al. 1994; Walters and Ludwig 1994; Adkison and Peterman 1996; Punt and Hilborn 1997) that biased priors can adversely affect fishery management performance. Priors for input parameters that are biased by as little as –50% for q or +100% for K can sharply increase risks of stock depletion even when priors are relatively diffuse. Curiously, positively biased priors for r reduced risks of stock depletion. This was mainly because of the implementation of a precautionary uncertainty adjustment. A positive bias in estimates of r resulted in a larger posterior SD in q and more precautionary action to be taken. In contrast, biased priors caused relatively small changes in average catches. For example, –50 and +100% biases in priors lead to no more than a 10% change in average catch.

Our results also corroborate recent concerns about the adverse effects of using overly precise priors (Walters and Ludwig 1994; Adkison and Peterman 1996). The use of precise priors in a stock assessment, even when the priors are unbiased in median and CV with respect to the prior used in the decision analysis, can adversely affect management performance. The main risk of an overly precise prior in a stock

© 1998 NRC Canada

assessment was the possibility that the actual value could be much more pessimistic than the most likely value in the stock assessment prior. The prior would tend to predominate in the initial years of management and to cause overestimation of the target quantities and overexploitation before the stock assessment homed in on the actual values.

In contrast, more diffuse priors (e.g., CV = 0.8) resulted in lower risks and lower average catches. This was mainly because of the effect of the harvest rate cap decision rule. Lower precision in the prior resulted in more precautionary action. The effects of precise versus diffuse priors were even more pronounced when the stock assessment priors were made more or less precise than the decision analysis posteriors. We therefore suggest that readers be cautious about using CVs < 0.5 for priors for parameters such as r, K, and q, especially when stock assessment data are relatively uninformative. Such advice appears to be appropriate even if empirical methods such as those that use data from similar populations (Gelman et al. 1995; Myers et al. 1996) suggest a prior CV that is less than 0.5. For example, there is always the risk that parameter value for the population of interest is in the tails of the distribution of the empirically derived prior. Use of a sharp prior in stock assessment would slow the rate of learning about the actual value. Thus, inappropriate management actions could be implemented for longer than if a more diffuse prior had been used.

Decision rules to achieve a precautionary approach

Finally, the application of a Bayesian decision analytic procedure has yielded some decision rules that could be useful for implementing a precautionary approach to managing developing fisheries (FAO 1995; Appendix 1). As mentioned before, the application of the management procedures designed to lower the risk of high harvest rates and to promote stock recovery when stock size is low can dramatically reduce the risk of overexploitation, yet cause little reduction in the average catch. Furthermore, when uncertainties are large, the harvest rate cap rule ensures that more precautionary actions are taken. The application of effort control rather than catch control rules can potentially reduce the risk of overexploitation without any reduction in average catch. Decision analysis results also show that the risk of overexploitation can be reduced also by avoiding the use of overly precise prior distributions.

Acknowledgments

This work was carried out as part of a project within the Fisheries Management Science Programme of the U.K. Department for International Development. David Agnew, Doug Butterworth, and Andre Punt are thanked for helpful comments on earlier drafts of this paper.

References

Adkison, M.D., and Peterman, R.M. 1996. Results of Bayesian methods depend on details of implementation: an example of estimating salmon escapements. Fish. Res. (Amst.), **25**: 155–170.

Berger, J.O. 1985. Statistical decision theory and Bayesian analysis. 2nd ed. Springer-Verlag, New York.

Bergh, M.O., and Butterworth, D.S. 1987. Toward rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. S. Afr. J. Mar. Sci. **5**: 937–951.

Butterworth, D.S., Cochrane, K.L., and de Oliveira, J.A.A. 1997. Management procedures: a better way to manage fisheries? The South African experience. *In* Global trends: fishery management. *Edited by* E.K. Pikitch, D.D. Huppert, and M.P. Sissenwine. Am. Fish. Soc. Symp. **20**: 83–90.

Clark, C.W., Charles, A.T., Beddington, J.R., and Mangel, M. 1985. Optimal capacity decisions in a developing fishery. Mar. Resour. Econ. **2**: 25–53.

Cordue, P.L., and Francis, R.I.C.C. 1994. Accuracy and choice of risk estimation for fisheries assessment. Can. J. Fish. Aquat. Sci. **51**: 817–829.

Food and Agriculture Organization of the United Nations (FAO). 1995. Part 1. Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Fish. Tech. Pap. 350/1.

Frederick, S.W., and Peterman, R.M. 1995. Choosing fisheries harvest policies: when does uncertainty matter? CanJ. Fish. Aquat. Sci. **52**: 291–306.

Garcia, S.M., and Newton, C. 1994. Current situation, trends and prospects in world capture fisheries. FAO Rep. D/T 4296.

Gelman, A., Carlin, J., Stern, H., and Rubin, D. 1995. Bayesian data analysis. Chapman and Hall, New York.

International Whaling Commission (IWC). 1992. Report of the Scientific Committee. Annex D. Management procedures. Rep. Int. Whaling Commn **42**: 87–136.

International Whaling Commission (IWC). 1994. Report of the Scientific Committee. Annex H. The revised management procedure (RMP) for baleen whales. Rep. Int. Whaling Commn **44**: 145–152.

Lapointe, M.F., Peterman, R.M., and MacCall, A.D. 1989. Trends in fishing mortality rate along with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis. Can. J. Fish. Aquat. Sci. **49**: 2129–2139.

McAllister, M.K., and Kirkwood, G.P. 1998. Bayesian stock assessment and policy evaluation: a review and example application using the logistic model. ICES J. Mar. Sci. **55**. In press.

McAllister, M.K., and Pikitch, E.K. 1997. A Bayesian approach to choosing a design for surveying fishery resources: application to the eastern Bering Sea trawl survey. Can. J. Fish. Aquat. Sci. **54**: 301–311.

McAllister, M.K., Pikitch, E.K., Punt, A.E., and Hilborn, R. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. Can. J. Fish. Aquat. Sci. **51**: 2673–2687.

Myers, R.A., Mertz, G., and Barrowman, N.J. 1996. Invariants of spawner–recruitment relationships for marine, anadromous, and freshwater species. Document prepared for the ICES Statistical Committee. ICES C.M. 1996/D:11.

Punt, A.E. 1997. The effects of future consumption by seals on catches of Cape hake off South Africa. *In* Global trends: fishery management. *Edited by* E.K. Pikitch, D.D. Huppert, and M.P. Sissenwine. Am. Fish. Soc. Symp. **20**: 134–140.

Punt, A.E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. **7**: 35–63.

Seber, G.A. 1982. The estimation of animal abundance and related parameters. Charles Griffin and Company Ltd., London, U.K.

Smith, A.D.M. 1993. Risks of over- and under-fishing new resources. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D.

© 1998 NRC Canada

Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 261–267.

Walters, C.J., and Ludwig, D. 1994. Calculation of Bayes posterior probability distributions for key population parameters: a simplified approach. Can. J. Fish. Aquat. Sci. **51**: 713–722.

Walters, C.J., and Maguire, J.J. 1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. **6**: 125–137.

Appendix 1. Summary of some guidelines for a precautionary approach to managing developing fisheries

In this appendix, we summarize some guidelines from a recent FAO report (FAO 1995) that could be used for achieving a precautionary approach to managing developing fisheries. The guidelines summarized below are ones pertinent to conducting decision analyses of alternative management actions that could be implemented and are recommended to be implemented before the onset of management. These are a small subset of the full set of guidelines for fishery management in FAO (1995). Other guidelines that are not reported below deal with establishing social and legal management frameworks for fisheries, implementation, enforcement, monitoring, and reevaluation, among other things.

Some of the main guidelines in FAO (1995) that deal with fisheries stock assessment and management include (1) using computer simulations to evaluate the consequences of alternative management actions that are designed to reduce the likelihood of undesirable outcomes such as overexploitation, (2) designing plans to mitigate possible undesirable outcomes from fishery development and using computer simulations to evaluate the potential effectiveness of the management actions, (3) designing management actions that account for uncertainty such that an acceptably low chance of overexploitation can be achieved when account is taken of uncertainties in stock assessment procedures, (4) considering long-term time scales of at least two to three decades for the assessment of the potential consequences of alternative management actions, (5) considering a range of alternative management actions that may differ in their basic approach such as effort control versus catch control options, (6) allowing catches to be as large as possible so long as the probability of substantial stock depletion is below an acceptably low level and catch can be kept reasonably steady, (7) establishing precautionary and preliminary biological reference points for management, (8) formulating decision rules that specify in advance which actions should be taken based on prespecified values for biological reference points for management, and (9) placing a conservative cap on both fishing capacity and the total fishing mortality rate. These guidelines were applied to the evaluations of alternative management procedures that were conducted in this paper.

Appendix 2. Delta method approximation of posterior variance in stock biomass

The variance, σ_B^2, in the logarithm of stock biomass, B_y, was approximated using the delta method (Seber 1982):

$$(2.1)\quad \sigma_B^2 \equiv \sum_{i=1}^{3} \hat{\sigma}_i^2 \left(\frac{\partial \log B_y}{\partial \theta_i} \right)_{|\mu_i}^2 + 2 \sum_{i<j} \sum \hat{\sigma}_{i,j} \left(\frac{\partial \log B_y}{\partial \theta_i} \right)_{|\mu_i} \times \left(\frac{\partial \log B_y}{\partial \theta_j} \right)_{|\mu_j}$$

where $\theta_1 = \log K$, $\theta_2 = \log r$, and $\theta_3 = \log q$, $\hat{\sigma}_i^2$ the estimated posterior variance for parameter θ_i, $\hat{\sigma}_{i,j}$ is the estimated posterior covariance between parameters θ_i and θ_j, and

$$\left(\frac{\partial \log B_y}{\partial \theta_i} \right)_{|\mu_i}$$

is the partial derivative of B_y with respect to θ_i evaluated at μ_i, the mean of θ_i. The μ_i was approximated by the posterior modal value for θ_i. The mode of the joint posterior for θ was found by nonlinear minimization of $-\log[p(\theta)L(\text{data}|\theta)]$. The partial derivatives

$$\left(\frac{\partial \log B_y}{\partial \theta_i} \right)_{|\mu_i}$$

were approximated numerically. The posterior variance–covariance matrix for θ_i was approximated from the negative inverse of the Hessian matrix with elements

$$\left(\frac{\partial \log[P(\theta|\text{data})]}{\partial \theta_i \partial \theta_j} \right)_{|\mu}$$

evaluated at the mode of the posterior for θ. Occasionally, the Hessian estimates were nonsensical, i.e., less than 0 or a very large number. We therefore set the variance in estimates to those in the previous year if at least one nonsensical estimate was obtained (i.e., that was less than 0 or greater than 4 (prior CV)^2).

© 1998 NRC Canada

An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae[1]

Pascal Sirois, Frédéric Lecomte, and Julian J. Dodson

Abstract: This study develops a new back-calculation method, based on the larvae of rainbow smelt (*Osmerus mordax*), that takes into account the variation of growth rate over time. Known-aged larvae were reared in four 60-L microcosms during 49 days in order to obtain a large range of individual growth trajectories. We first validated the daily nature of the otolith increment deposition rate. The proposed time-varying growth (TVG) method weights the contribution of each increment in the length calculation using a growth effect factor. A small growth increment contributes less to the length increase of larvae than its relative importance in total otolith growth. On the other hand, a large growth increment contributes more to the length increase of larvae in comparison with its relative importance in total otolith growth. This method provided significantly better estimates of previous length-at-age than the biological intercept (BI) method at the individual level. In addition, the TVG method tended to provide more accurate estimates of previous length-at-age than the BI method at the population level, but the difference was not significant. The importance of using the TVG method instead of the BI method to back-calculate individual and population growth trajectories increases with the magnitude of the growth effect and the variation in growth rates over time.

Résumé : Cette étude présente une nouvelle méthode de rétrocalcul qui tient compte des variations temporelles du taux de croissance observées chez des larves d'éperlan arc-en-ciel (*Osmerus mordax*). Des larves d'un âge connu ont été élevées dans quatre microcosmes de 60 L pendant 49 jours dans le but d'obtenir un large éventail de trajectoires de croissance. Nous avons préalablement validé le dépôt journalier des accroissements sur les otolithes. La méthode des variations temporelles du taux de croissance (TVG) que nous proposons, corrige la contribution de chaque accroissement dans le calcul de la longueur en utilisant un facteur d'effet de croissance. Un petit accroissement contribue moins à l'augmentation de la longueur de la larve que son importance relative dans la taille de l'otolithe. De façon opposée, un grand accroissement contribue plus à l'augmentation de la longueur de la larve que son importance relative dans la taille de l'otolithe. Au niveau individuel, la méthode TVG a fourni de meilleures estimations de longueurs à des âges ultérieurs que la méthode de l'ordonnée à l'origine biologique (BI). De plus, au niveau des populations, la méthode TVG avait tendance à fournir de meilleures estimations de longueurs à des âges ultérieurs que la méthode BI, cependant la différence n'est pas significative. L'importance d'utiliser la méthode TVG au lieu de la méthode BI pour rétrocalculer les trajectoires de croissance des individus et des populations, croît avec l'augmentation de l'effet de croissance et des variations temporelles du taux de croissance.

Introduction

Back-calculation of fish lengths from bony structures has provided major contributions to fishery ecology by permitting the collection of individual longitudinal data series. Such series have been widely used to determine factors controlling recruitment. These studies focus on young individuals because small changes in their survival can lead to great variations in recruitment (Houde 1987).

Received May 22, 1998. Accepted October 16, 1998.
J14599

P. Sirois, F. Lecomte, and J.J. Dodson.[2] GIROQ, Département de Biologie, Université Laval, Québec, QC G1K 7P4, Canada.

[1]Contribution to the program of GIROQ (Groupe Interuniversitaire de Recherches Océanographiques du Québec).

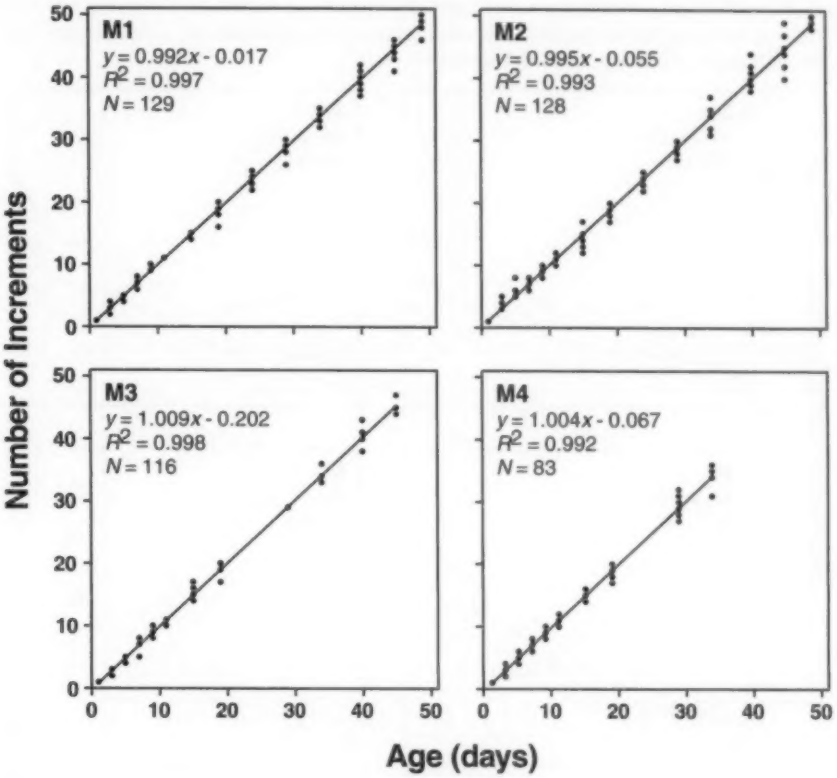
[2]Author to whom all correspondence should be addressed. e-mail: julian.dodson@bio.ulaval.ca

Since the first utilization of back-calculation (Lea 1910), numerous methods have been developed to enhance length estimates (see review by Francis 1990). Most of these methods are based on two assumptions: (*i*) constant periodicity in the formation of the bony structure and (*ii*) proportionality between the growth of calcified structures and somatic growth. The first assumption has been demonstrated on daily and annual bases for a wide variety of fish species (Campana and Neilson 1985; Casselman 1987; Geffen 1992). It is nevertheless recommended that the deposition rate for each studied species be validated. The second assumption has never been demonstrated directly, but rather empirically using strong correlations between the size of the bony part and the size of the fish.

Many investigators have reported that the relationship between fish size and otolith size is at times weak or "uncoupled" (Marshall and Parker 1982; Volk et al. 1984; Rice et al. 1985; Mosegaard et al. 1988; Molony and Choat 1990; Wright et al. 1990; Bradford and Geen 1992; Secor and Dean 1992). The relationship between somatic growth and otolith growth has been demonstrated to be related to abso-

© 1998 NRC Canada

Fig. 1. Relationships between number of increments and age of individual rainbow smelt larvae sampled in four different microcosms (M1, M2, M3, and M4). Regression equations, R^2 values, and sample size (N) are reported on each graph. All panels are scaled similarly.



lute growth rate (Reznick et al. 1989; Secor and Dean 1989, 1992; Secor et al. 1989; Francis et al. 1993; Xiao 1996; Schirripa and Goodyear 1997). According to these studies, otoliths from slow-growing fish are larger than those from fast-growing fish of the same size. This phenomenon has been called the growth effect and may cause bias in length estimates when using traditional back-calculation methods (Campana 1990; Campana and Jones 1992). Campana (1990) proposed a biological intercept (BI) method to eliminate back-calculation bias caused by the growth effect. However, it has been shown that this method is sensitive to variations in growth rate over time (Campana 1990; Secor and Dean 1992). Growth rate variations are likely to appear during larval and juvenile stages owing to environmental variation or transition between early developmental stages.

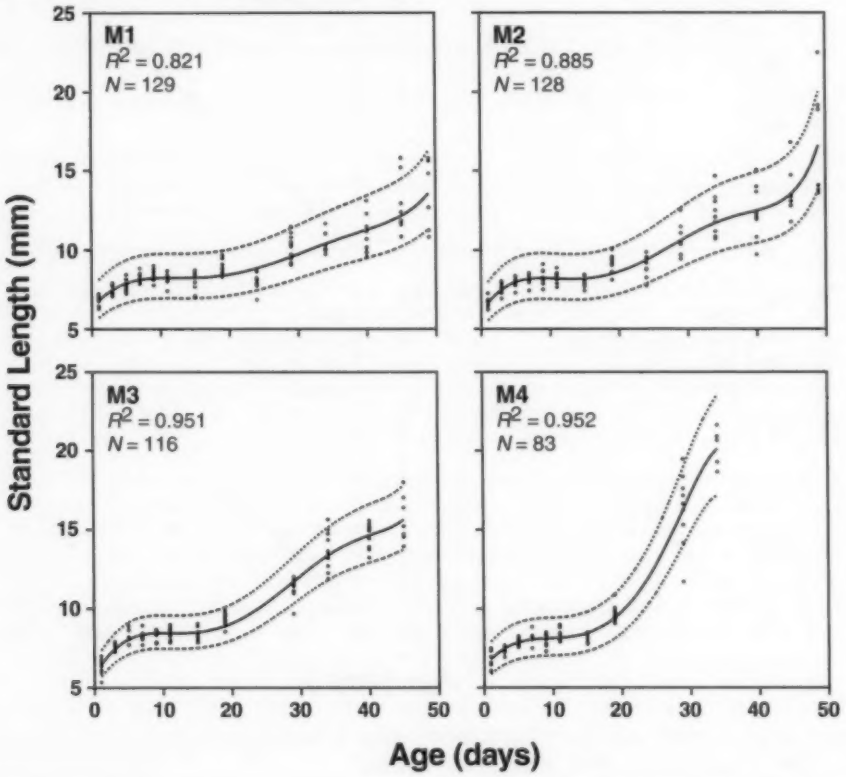
The principal objective of this study was to develop a new back-calculation method, based on the larvae of rainbow smelt (*Osmerus mordax*), that takes into account the variation of growth rate over time. This method is based on the assumptions that (*i*) there is a daily periodicity in the formation of the otolith and (*ii*) there is a proportionality between somatic and otolith growth. However, the method assumes that the proportionality varies with somatic growth rate. Thus, the first step was to validate the otolith increment deposition rate for rainbow smelt larvae. We then developed an equation that weighted the contribution of each increment in the length calculation using a growth effect factor. Finally, we compared back-calculated lengths estimated using the proposed time-varying growth (TVG) method with those obtained with the BI method at the population level and at the individual level.

Table 1. Number of larvae sampled in microcosms on various dates.

Date	Days after hatch	No. of larvae sampled			
		M1	M2	M3	M4
May 24	1	10	10	10	10
May 26	3	10	10	10	10
May 28	5	10	10	10	10
May 30	7	10	10	10	10
June 1	9	10	10	10	10
June 3	11	10	10	10	10
June 7	15	10	10	10	10
June 11	19	10	10	10	10
June 16	24	10	10		
June 21	29	10	10	10	10
June 26	34	10	10	10	6
July 2	40	10	10	10	
July 7	45	10	10	7	
July 11	49	8	6		

© 1998 NRC Canada

Fig. 2. Observed standard length of individual rainbow smelt sampled at various ages in M1, M2, M3, and M4 with respective polynomial lines (solid lines) fit to the natural log-transformed data. M1: $\ln(y) = 1.85 + 0.0729x - 0.00764x^2 + 0.000358x^3 - 0.00000723x^4 + 0.0000000533x^5$; M2: $\ln(y) = 1.80 + 0.101x - 0.0120x^2 + 0.000625x^3 - 0.0000137x^4 + 0.000000108x^5$; M3: $\ln(y) = 1.77 + 0.116x - 0.0133x^2 + 0.000673x^3 - 0.0000144x^4 + 0.000000110x^5$; M4: $\ln(y) = 1.85 + 0.0792x - 0.00919x^2 + 0.000436x^3 - 0.00000604x^4$. The 95% confidence curves for individual estimates (dotted lines) are shown for each microcosm. R^2 values and sample size (N) are reported on each graph. All panels are scaled similarly.



Materials and methods

Experimental procedure

A microcosm experiment was performed in order to obtain a large range of individual growth trajectories. Fertilized eggs of rainbow smelt were provided by an experimental incubator operated by the Ministère de l'Environnement et de la Faune (MEF, Quebec) on a well-known spawning site of this species (Ruisseau de l'Église, Beaumont, Quebec). On May 23, 1994, at night, large numbers of larvae hatched and were placed randomly in four 60-L microcosms (M1, M2, M3, and M4; height 55 cm, diameter 40 cm). Initial density of larvae varied from 16 to 22 ind.·L^{-1}. Known-age larvae were reared for 49 days. Microcosms were supplied with water pumped directly from the south shore of the St. Lawrence middle estuary. This region constitutes a major nursery area for rainbow smelt (Dodson et al. 1989; Laprise and Dodson 1989*a*, 1989*b*). Environmental conditions were similar among microcosms, but varied in time according to the natural changes of the variables in the wild. Temperature warmed gradually from 10.2 to 22.0°C, salinity fluctuated between 0 and 2.1 psu (practical salinity units), and turbidity ranged between 55 and 78 NTU (nephelometric turbidity units) during the experiment.

Natural food was present in the inflow water but was not sufficient to support the densities of larvae in the microcosms. Rations of wild-caught zooplankton were added to the tanks in order to account for higher larval densities. A ration (about 900 prey items) was added once per day in M1, twice per day in M2, three times per day in M3, and four times per day in M4.

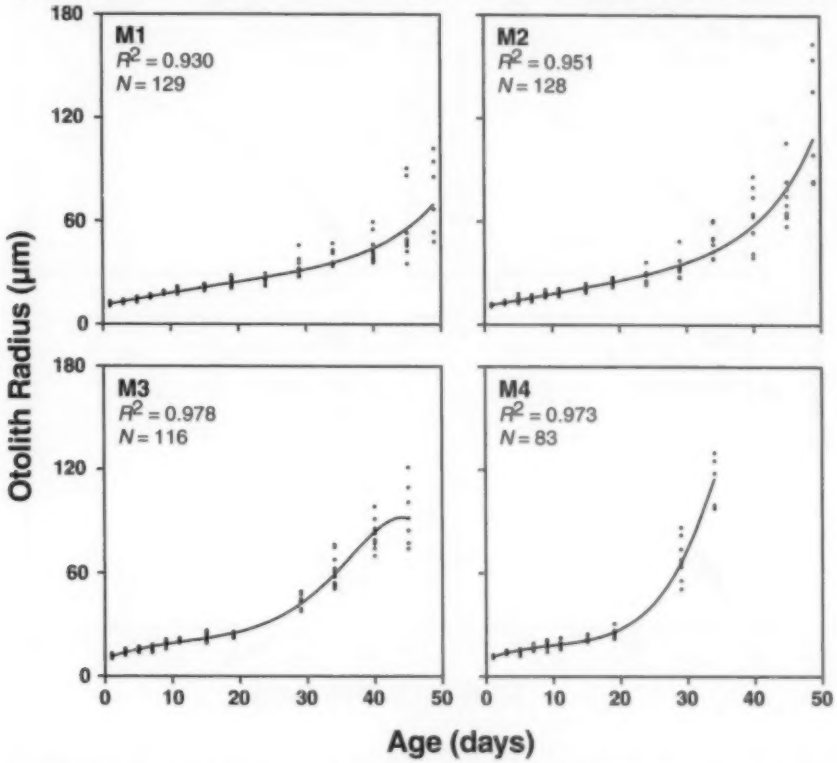
Larvae were sampled at 2- to 6-day intervals (Table 1) and were preserved in 95% ethanol. Standard lengths were measured using an image analysis system. Shrinkage due to preservation in 95% ethanol was calculated on 30 rainbow smelt larvae ranging in length from 6.14 to 15.86 mm. Shrinkage varied from –7.04 to 5.33% and the mean was –1.12%. The 95% confidence interval around this mean ranged from –2.29 to 0.04% and thus was not significantly different from 0. For this reason, no correction for shrinkage due to preservation in ethanol was made.

Otolith microstructure procedure

Sagittal otoliths were removed with fine needles and mounted on a microscope slide with thermoplastic glue (Crystal Bond). Rainbow smelt larvae sagittae are small (mean otolith radius at hatching = 10.38 μm) and show clear and distinct growth increments. Otoliths were measured using an image analysis system connected to a light microscope at 630–1000× magnification. Three measurements were taken along the growth axis: core radius (micrometres), otolith radius (micrometres), and individual increment width (micrometres). The number of increments was automatically compiled using the number of widths measured. All otoliths were read in random order by two different readers. A total

© 1998 NRC Canada

Fig. 3. Observed otolith radius of individual rainbow smelt sampled at various ages in M1, M2, M3, and M4 with respective polynomial lines fit to the natural log-transformed data. M1: $\ln(y) = 2.41 + 0.0623x - 0.00154x^2 + 0.0000211x^3$; M2: $\ln(y) = 2.39 + 0.0623x - 0.00141x^2 + 0.0000224x^3$; M3: $\ln(y) = 2.34 + 0.113x - 0.00766x^2 + 0.000275x^3 - 0.00000303x^4$; M4: $\ln(y) = 2.32 + 0.126x - 0.0112x^2 + 0.000493x^3 - 0.00000619x^4$. R^2 values and sample size (N) are reported on each graph. All panels are scaled similarly.



of 487 otoliths were examined and 31 (6.3%) were discarded from the analysis because of a discrepancy exceeding 10% in the number of increments between readers.

Computations

Computations involving standard length and otolith radius were executed on natural log-transformed data. The growth effect (R) was calculated by a linear regression using each individual fish as an independent observation (N = 456):

$$(1) \qquad S = b + RG$$

where S is the estimated slope of the fish size – otolith size relationship, G is the absolute linear growth rate in fish length, and b and R (growth effect) are estimated parameters of the linear regression. For each fish, S was computed using standard length and otolith radius observed at capture, and standard length and otolith radius at hatching, which is the BI (see below). Similarly, G was calculated as the difference between the observed standard length at capture and the standard length at hatching divided by the number of daily growth increments obtained from otoliths.

All fish (N = 456) were used in the back-calculation analysis. For each fish, the body growth trajectory was back-calculated on every day lived in the microcosms using two different methods. First, the BI method provided length estimates using the following equation (Campana 1990):

$$(2) \qquad L_t = L_c + (O_t - O_c)(L_c - L_0)(O_c - O_0)^{-1}$$

where L is fish length at age t (L_t), at the BI (L_0), and at capture (L_c) and O is otolith radius at age t (O_t), at the BI (O_0), and at capture (O_c). To determine L_0, measurements of rainbow smelt larvae within hours after hatching were recorded from an independent sample in the laboratory in 1995 and 1996. The mean standard length calculated on newly hatched rainbow smelt was 5.81 mm (SD = 0.41, N = 315). The O_0 was estimated using the observed core radius on the otolith of each larva.

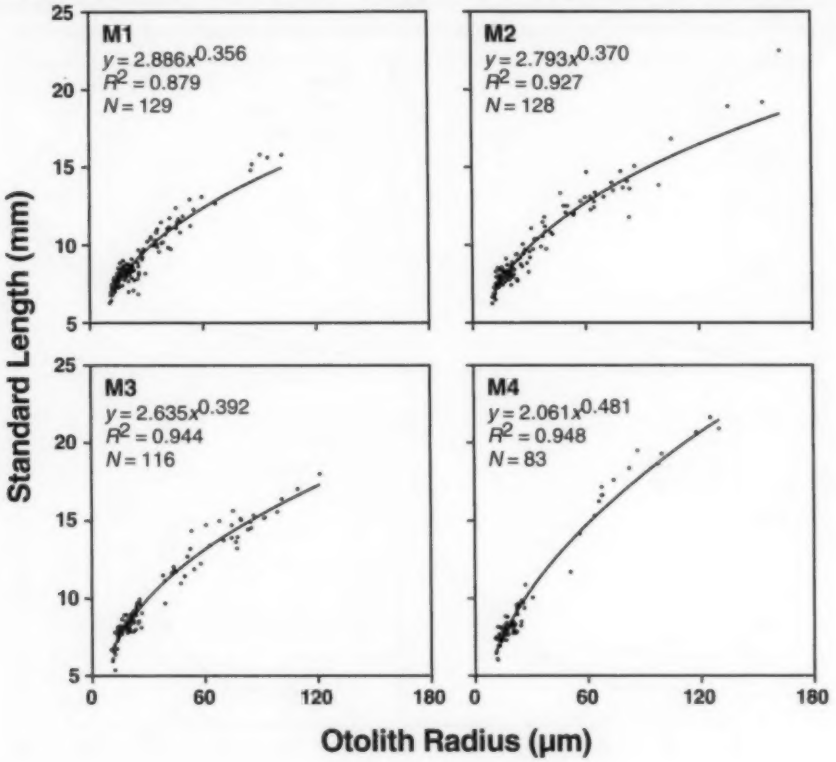
The second method was developed using the structure of the BI method and a TVG simulation presented by Campana (1990). This method involves calculating a growth effect factor to correct the contribution of each increment to the body growth trajectory. Back-calculated lengths according to the TVG method were provided by

$$(3) \qquad L_t = L_0 + \sum_{i=1}^{t} (W_i + R(W_i - W))(L_c - L_0)(O_c - O_0)^{-1}$$

where W_i is the increment width at age t and W is the mean increment width. Values of W were calculated for each fish during the yolk-sac stage (0–7 days), preflexion stage (8–30 days), and postflexion stage (31+ days). Developmental stages were determined in this study by laboratory observations and by the description of larval rainbow smelt development of Cooper (1978). Since rainbow smelt larvae reach the juvenile stage at about 36 mm, no larva became juvenile in this study.

© 1998 NRC Canada

Fig. 4. Relationships between standard length and otolith radius of individual rainbow smelt sampled at various ages in M1, M2, M3, and M4. Regression equations, R^2 values, and sample size (N) are reported on each graph. All panels are scaled similarly.



Statistical analysis

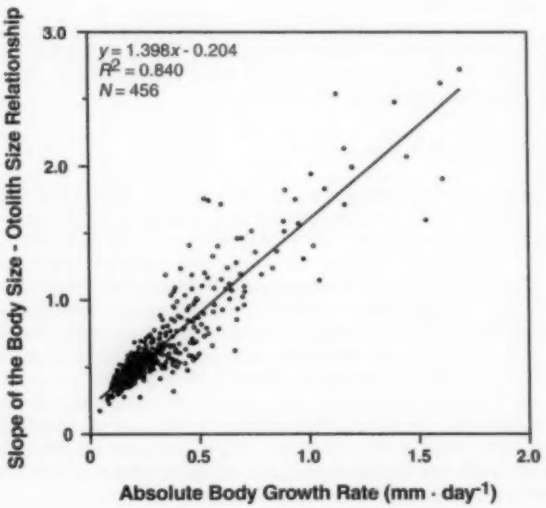
Regression slopes (number of increments versus age; mean back-calculated length versus mean observed length) were compared with the theoretical slope of 1 with a t-test using $\alpha = 0.05$ as the level of significance. The 95% confidence curves for individual estimates of the polynomial regression were calculated according to Neter et al. (1985). Slopes and elevations of the fish size – otolith size relationships were compared using an analysis of covariance (ANCOVA) and a Tukey multiple comparisons test (Zar 1987). Frequencies of back-calculated lengths observed within the 95% confidence curves of the fitted growth model were compared using a contingency table (Zar 1987).

Results

Validation of daily otolith increment deposition rate

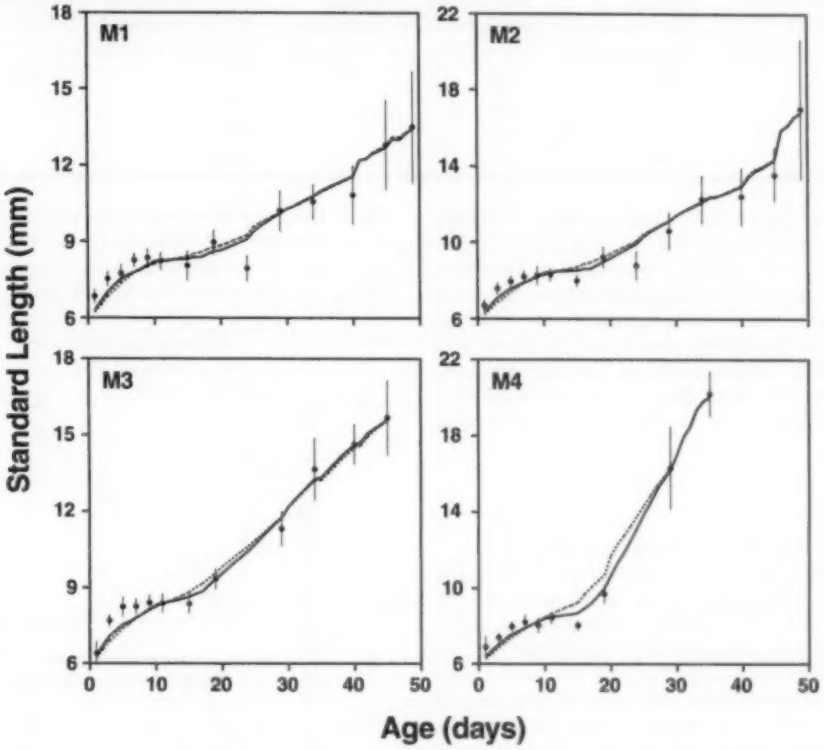
Relationships between the number of increments and true age of the rainbow smelt larvae are shown for each microcosm in Fig. 1. Deposition rates, i.e., slopes of regressions, varied from 0.992 to 1.009 increments per day and were not significantly different from 1 in M1, M2, and M4. The slope of the regression is statistically different from 1 in M3 ($t_{114} = 1.995$, $p = 0.048$). However, this corresponds to one additional growth increment produced every 110 days, which is trivial. Intercepts were not significantly different from 0 in all microcosms ($p > 0.05$ in all cases). This result suggested that daily increment formation began at hatching,

Fig. 5. Relationship between the slope of the body size – otolith size relationship and the absolute body growth rate calculated using individual larvae sampled at various dates in M1, M2, M3, and M4. All larvae from all microcosms are pooled on the same graph.



© 1998 NRC Canada

Fig. 6. Mean somatic growth trajectories as showed by the observed length (circles), the back-calculated length using the BI method (dotted lines), and the back-calculated length using the TVG method (solid lines) in M1, M2, M3, and M4. Vertical bars on observed lengths represent the SDs.



as confirmed by analysis of otolith microstructure of larvae sampled on day 1.

Mean somatic and otolith growth trajectories

Mean somatic growth trajectories within microcosms based on length at capture were described best by fourth-order (M4) and fifth-order (M1, M2, and M3) natural log-transformed equations (Fig.2). These population growth trajectories showed variations in growth rates over time. Among microcosms, fluctuations were similar; fast growth during the yolk-sac stage (0–7 days) was followed by a slow initiation of a curvilinear exponential-type growth period after yolk absorption (Fig. 2). Mean otolith growth trajectories within microcosms based on radius at capture were described best by third-order (M1 and M2) and fourth-order (M3 and M4) natural log-transformed equations (Fig. 3).

Body size – otolith size relationships and the growth effect

Power curves were fitted to the relationships between standard length and otolith radius (Fig. 4). ANCOVA indicated a significant difference among regression slopes ($F_{3,448} = 24.33$, $p < 0.0001$). Multiple comparisons showed a significant difference between all microcosms except between M1 and M2 ($p > 0.05$ for slope and elevation) and between M2 and M3 ($p > 0.05$ for slope and elevation). Differences in slopes of these relationships suggested the presence of a growth effect. According to eq. 1, the magnitude of the growth effect was estimated to be 1.398 (Fig. 5).

Comparison of the TVG method with the BI method at the population level

Mean somatic growth trajectories in the microcosms, as calculated with the TVG method, were higher during the yolk-sac stage and lower between ages 13 and 29 than those calculated with the BI method (Fig. 6). Mean back-calculated length-at-age estimated with the BI method varied from –10.5 to +16.3% of the mean observed length-at-age in microcosms (Fig. 6). Mean back-calculated length-at-age estimated with the TVG method varied from –8.7 to +14.5% of the mean observed length-at-age in microcosms (Fig. 6). These observations suggested that the TVG method described more realistically the observed mean somatic growth trajectories in microcosms. However, there is no significant difference between the slope describing the relationship between mean back-calculated length estimates and mean observed lengths and the theoretical slope of 1 for both methods (Fig. 7).

Comparison of the TVG method with the BI method at the individual level

The number of individual length estimates included within the 95% confidence curves of the fitted growth model was higher when using the TVG method than when using

© 1998 NRC Canada

Table 2. Number of back-calculated length estimates (or increments) included within the 95% confidence curves for individual estimates of the fitted growth curve (Fig. 2) in each microcosm.

	No. of larvae used for back-calculation	Total no. of back-calculated length estimates	No. of length estimates within the 95% confidence curves using the BI method	No. of length estimates within the 95% confidence curves using the TVG method	p
M1	129	2452	2325	2339	ns
M2	128	2524	2306	2338	ns
M3	116	2011	1779	1822	0.0268
M4	83	1079	875	946	<0.0001

the BI method in all microcosms (Table 2). This difference is significantly different in M3 (χ^2 = 4.91, df = 1, p = 0.0268) and M4 (χ^2 = 17.72, df = 1, $p < 0.0001$). Moreover, individual growth trajectories from older larvae calculated with the TVG method fitted more accurately the observed mean somatic growth trajectories than those calculated with the BI method in all microcosms (Fig. 8). The maximum difference between the two methods for a single length estimate on a specific day was 39%, based on one larva aged 17 days in M4.

Discussion

Validation of daily otolith increment deposition rate

This study validated the daily nature of otolith increment deposition rate in rainbow smelt larvae. In addition, our observations showed that daily increment formation started at hatching in this species and under these conditions. Examination of otoliths from known-age larvae is one of the most rigorous and reliable methods for validating daily increment deposition (Geffen 1992). Our results differed from the observations of a closely related species, the European smelt (*Osmerus eperlanus*) (Sepúlveda 1994). Using the marginal increment technique on wild-caught larvae, Sepúlveda (1994) assumed that the first discontinuous zone corresponds to the first feeding check.

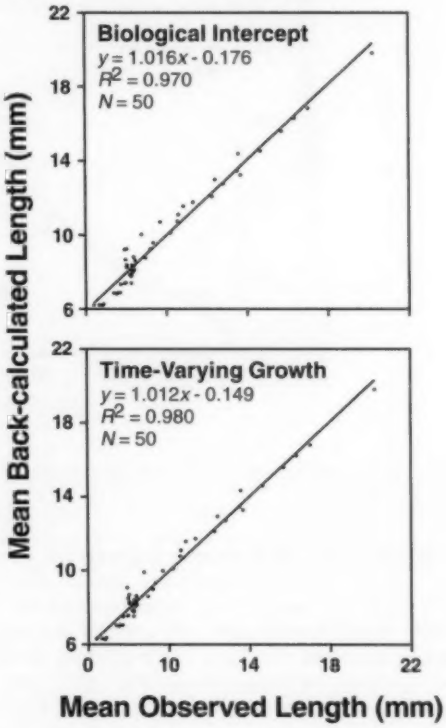
Comparison of the TVG method with the BI method

This study suggested that the TVG method provided accurate length estimates at previous ages at both the population and individual levels. The TVG method weighted the contribution of each increment in the length calculation using a growth effect factor ($R(W_t - W)$, eq. 3). A small growth increment contributed less to the length increase of larvae than its relative importance in total otolith growth. On the other hand, a large growth increment contributed more to the length increase of larvae in comparison with its relative importance in total otolith growth. The degree of correction is a function of the variation of increment widths and (or) of the magnitude of the growth effect. In the absence of variable increment widths and (or) growth effect, the TGV method corresponds exactly to the BI method.

The proposed model is analogous to proportional-type back-calculation methods as opposed to regression-type methods (see review by Francis 1990). The latter do not allow individual deviation from the mean growth history and do not take into account observed length at capture. In proportional methods, especially when using a BI, the starting and end points of the growth trajectory are reliable. This is important for individual estimations. The use of otolith analysis and the individual-based approach in fishery ecology allows one to perform longitudinal studies and may provide important insights into the recruitment processes. For instance, the analysis of otoliths of survivors can identify the life history stage critical to the determination of the year-class strength. Identification of the stage that is most important for year-class determination allows us to focus on the particular mechanism important to recruitment success (Sissenwine 1984). This study illustrated that the TVG method provided accurate individual length estimates and should be useful for the individual-based approach.

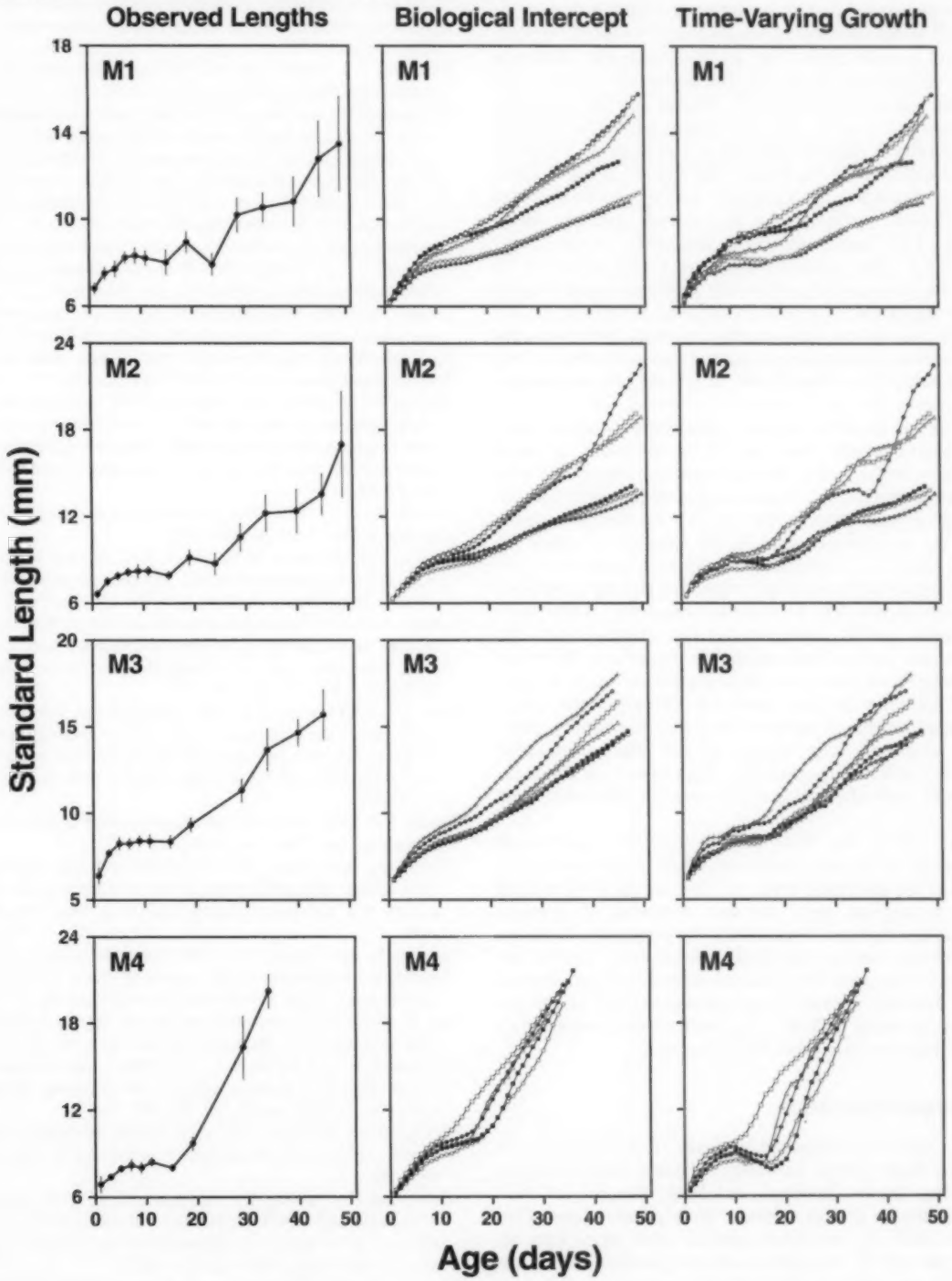
The TVG method demonstrated two desirable characteristics. First, it accounted for variations in growth rates over time by including the growth effect in the back-calculation formula. Campana (1990, eq. 7) presented a regression-type equation to correct TVG; however, when applied to our data

Fig. 7. Relationship between mean back-calculated length and mean observed length using the BI and TVG methods. The four microcosms are pooled. Regression equations, R^2 values, and sample size (N) are reported on each graph.



© 1998 NRC Canada

Fig. 8. Observed mean somatic growth trajectories with SDs and back-calculated individual growth trajectories for older larvae in M1, M2, M3, and M4 according to the BI method and TVG methods. Within one microcosm, similar symbols in the middle and the right panels correspond to the same individual. All panels are scaled similarly.



© 1998 NRC Canada

using averaged parameters (L_0 = 5.81 mm, k = 0.65 mm·μm^{-1}, R = 1.4, W for days 1–7 = 1.18 μm, W for days 8+ = 1.27 μm), this equation performed poorly. Deviation of the mean somatic growth trajectories from lengths observed in the microcosms varied from 0 to 693%. Second, the TVG method allows one to mathematically determine periods of negative growth. Otolith deposition rate is a conservative process (Mugiya 1987; Mugiya and Oka 1991). In the absence of somatic growth or during periods of negative somatic growth, calcium deposition continues at a reduced rate (Mugiya 1990). Although this feature is particularly useful to obtain true age estimates, it creates errors in length back-calculation when using proportional methods. However, the TVG method is able to accurately estimate negative growth. The quadratic response model proposed by Secor and Dean (1992) accurately predicted mean somatic growth trajectories of larvae reared in the laboratory including inflexion points and negative growth. However, that model was a regression-type method and performed poorly when applied to an independent sample of pond-reared larvae.

The use of the TVG method requires a continuous series of increment widths from the BI to the point of back-calculation, which can be time-consuming to those who wish to back-calculate only a small portion of the early life history (e.g., estimation of recent growth). Another characteristic of the proposed method is the manner in which the growth effect is incorporated into the back-calculation procedure. Secor and Dean (1992) suggested that the growth effect is not expected to be constant across life stages. Hare and Cowen (1995) recommended incorporating such life stage effects in the back-calculation procedures. However, the growth effect is the best single variable available to summarize growth variations across all developmental stages and should not be recalculated for every life history stage. Instead of using a stage-specific growth effect, the method developed here incorporates life stage effects in the back-calculation method by using a stage-specific mean increment width.

In this study, the TVG method provided significantly better estimates for back-calculated length-at-age than the BI method at the individual level. In addition, the TVG method tended to provide more accurate estimates of previous length-at-age than the BI method at the population level, but the difference was not significant. We conclude that the importance of using the TVG method instead of the BI method to back-calculate individual and population body growth trajectories increases with the magnitude of the growth effect and the variation in growth rates over time.

Acknowledgements

This project was supported by grants from the NSERC to J.J.D. We thank Hélène Lemieux, Normand Bertrand, Elizabeth Long, Denis Thivierge, and Serge Higgins for their valuable help in this experiment. We especially thank Guy Trencia (MEF) for providing rainbow smelt eggs. John M. Casselman and an anonymous referee provided helpful reviews on an earlier version of the manuscript. P.S. was funded by NSERC, FCAR (Quebec), and GIROQ fellowships.

References

Bradford, M.J., and Geen, G.H. 1992. Growth estimates from otolith increment widths of juvenile chinook salmon (*Oncorhynchus tshawytscha*) reared in changing environments. J. Fish Biol. **41**: 825–832.

Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. **47**: 2219–2227.

Campana, S.E., and Jones, C.M. 1992. Analysis of otolith microstructure data. *In* Otolith microstructure examination and analysis. *Edited by* D.K. Stevenson and S.E. Campana. Can. Spec. Publ. Fish. Aquat. Sci. No. 117. pp. 73–100.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. **42**: 1014–1032.

Casselman, J.M. 1987. Determination of age and growth. *In* The biology of fish growth. *Edited by* A.H. Weatherley and H.S. Gill. Academic Press, New York. pp. 209–242.

Cooper, J.E. 1978. Identification of eggs, larvae, and juveniles of the rainbow smelt, *Osmerus mordax*, with comparisons to larval alewife, *Alosa pseudoharengus*, and gizzard shad, *Dorosoma cepedianum*. Trans. Am. Fish. Soc. **107**: 56–62.

Dodson, J.J., Dauvin, J.-C., Ingram, R.G., and D'Anglejan, B. 1989. Abundance of larval rainbow smelt (*Osmerus mordax*) in relation to the maximum turbidity zone and associated macroplanktonic fauna of the middle St. Lawrence Estuary. Estuaries, **12**: 66–81.

Francis, R.I.C.C. 1990. Back-calculation of fish length: a critical review. J. Fish Biol. **36**: 883–902.

Francis, M.P., Williams, M.W., Pryce, A.C., Pollard, S., and Scott, S.G. 1993. Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). Fish. Bull. U.S. **91**: 159–164.

Geffen, A.J. 1992. Validation of otolith increment deposition rate. *In* Otolith microstructure examination and analysis. *Edited by* D.K. Stevenson and S.E. Campana. Can. Spec. Publ. Fish. Aquat. Sci. No. 117. pp. 101–113.

Hare, J.A., and Cowen, R.K. 1995. Effect of age, growth rate, and ontogeny on the otolith size – fish size relationship in bluefish, *Potamus saltatrix*, and the implications for back-calculation of size in fish early life history stages. Can. J. Fish. Aquat. Sci. **52**: 1909–1922.

Houde, E.D. 1987. Fish early life history dynamics and recruitment variability. Am. Fish. Soc. Symp. **2**: 17–29.

Laprise, R., and Dodson, J.J. 1989*a*. Ontogeny and importance of tidal vertical migrations in the retention of larval smelt *Osmerus mordax* in a well-mixed estuary. Mar. Ecol. Prog. Ser. **55**: 101–111.

Laprise, R., and Dodson, J.J. 1989*b*. Ontogenic changes in the longitudinal distribution of two species of larval fish in a turbid well-mixed estuary. J. Fish Biol. **35**(Suppl. A): 39–47.

Lea, E. 1910. On the methods used in the herring-investigations. Publ. Circons. Cons. Perm. Int. Explor. Mer. No. 53.

Marshall, S.L., and Parker, S.S. 1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. Can. J. Fish. Aquat. Sci. **39**: 542–547.

Molony, B.W., and Choat, J.H. 1990. Otolith increment widths and somatic growth rate: the presence of a time-lag. J. Fish Biol. **37**: 541–551.

Mosegaard, H., Svedäng, H., and Taberman, K. 1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. **45**: 1514–1524.

Mugiya, Y. 1987. Phase difference between calcification and organic matrix formation in the diurnal growth of otoliths in the rainbow trout, *Salmo gairdneri*. Fish. Bull. U.S. **85**: 395–401.

© 1998 NRC Canada

Mugiya, Y. 1990. Long-term effects of hypophysectomy on the growth and calcification of otoliths and scales in the goldfish, *Carassius auratus*. Zool. Sci. (Tokyo), **7**: 273–279.

Mugiya, Y., and Oka, H. 1991. Biochemical relationship between otolith and somatic growth in the rainbow trout *Oncorhynchus mykiss*: consequence of starvation, resumed feeding, and diel variations. Fish. Bull. U.S. **89**: 239–245.

Neter, J., Wasserman, W., and Kutner, M.H. 1985. Applied linear statistical models: regression, analysis of variance, and experimental designs. 2nd ed. R.D. Irwin, Homewood, Ill.

Reznick, D., Lindbeck, E., and Bryga, H. 1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. **46**: 108–112.

Rice, J.A., Crowder, L.B., and Binkowski, F.P. 1985. Evaluating otolith analysis for bloater *Coregonus hoyi*: do otoliths ring true? Trans. Am. Fish. Soc. **114**: 532–539.

Schirripa, M.J., and Goodyear, C.P. 1997. Simulation of alternative assumptions of fish otolith–somatic growth with a bioenergetic model. Ecol. Model. **102**: 209–223.

Secor, D.H., and Dean, J.M. 1989. Somatic growth effects on the otolith – fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. **46**: 113–121.

Secor, D.H., and Dean, J.M. 1992. Comparison of otolith-based back-calculation methods to determine individual growth histories of larval striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. **49**: 1439–1454.

Secor, D.H., Dean, J.M., and Baldevarona, R.B. 1989. Comparison of otolith growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationships. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 431–438.

Sepúlveda, A. 1994. Daily growth increments in the otoliths of European smelt *Osmerus eperlanus* larvae. Mar. Ecol. Prog. Ser. **108**: 33–42.

Sissenwine, M.P. 1984. Why do fish populations vary? *In* Exploitation of marine communities. *Edited by* R.M. May. Springer-Verlag, New York. pp. 59–94.

Volk, E.C., Wissmar, R.C., Simentad, C.A., and Eggers, D.M. 1984. Relationship between otolith microstructure and the growth of juvenile chum salmon (*Oncorhynchus keta*) under different prey rations. Can. J. Fish. Aquat. Sci. **41**: 126–133.

Wright, P.J., Metcalfe, N.B., and Thorpe, J.E. 1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. J. Fish Biol. **36**: 241–249.

Xiao, Y. 1996. How does somatic growth rate affect otolith size in fishes? Can. J. Fish. Aquat. Sci. **53**: 1675–1682.

Zar, J.H. 1987. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.

© 1998 NRC Canada

PERSPECTIVES

Intercalibration of research survey vessels in fisheries: a review and an application

D. Pelletier

Abstract: Fisheries stock assessments often rely on time series of abundance indices obtained from annual research surveys. It is thus important to maintain the temporal continuity of such series when vessels change. This can be achieved by estimating conversion coefficients between the two vessels through an intercalibration experiment. This paper describes such an experiment conducted from two French research vessels, including (*i*) a review of previous intercalibration experiments; (*ii*) a statistical model based on quasi-likelihood functions yielding conversion coefficient estimators; (*iii*) a simulation approach using both the model and previous survey data to plan the experiment; and (*iv*) a bootstrap procedure providing robust estimates of the conversion coefficients obtained from the model.

Résumé : L'évaluation des stocks halieutiques utilise souvent les séries temporelles d'indices d'abondance obtenus lors de campagnes annuelles. Il est donc important de conserver la cohérence temporelle de ces séries au moment d'un changement de navire de recherche. Ceci peut se faire en estimant des coefficients de conversion entre les deux navires grâce à une expérience d'intercalibration. Cet article décrit une expérience de ce type menée entre deux navires français, en présentant notamment : (*i*) une revue des expériences d'intercalibration déjà réalisées ; (*ii*) un modèle statistique basé sur des fonctions de quasi-vraisemblance qui permet d'obtenir des estimateurs des coefficients de conversion ; (*iii*) des simulations à partir du modèle et de données de campagne passées afin de planifier l'expérience ; et (*iv*) une procédure de bootstrap qui fournit des estimations robustes des coefficients de conversion obtenus par le modèle.

Introduction

Scientific surveys are an important source of information for estimating the abundance of populations in fisheries science. Many stock assessments rely partially or sometimes mainly on time series of abundance indices obtained from annual surveys. The temporal continuity of such time series may be hindered by a change in survey vessel or in fishing equipment.

Indeed, the catch resulting from any fishing operation can be considered dependent on three factors: (*i*) vessel and fishing characteristics, e.g., fishing gear, technological equipment, crew, etc.; (*ii*) characteristics of sampled populations, e.g., abundance level, spatial distribution, availability to fishing; and (*iii*) environmental conditions, e.g., weather, hydrology, depth, and substrate type. It is necessary to identify and, if possible, separate these three effects to correctly interpret catch data. Otherwise, for example, changes in fishing power may be interpreted as changes in resource availability or abundance, resulting in an inaccurate assessment of the resources. In the case of bottom-trawl surveys, the characteristics of the vessel that were likely to influence its performance were previously discussed in a workshop in Canada in 1980 (Doubleday and Rivard 1981, see in particular Azarovitz (1981), Byrne et al. (1981), Carrothers (1981), and Foster et al. (1981)). Most of these authors pointed out that a large proportion of the variability in catches could be attributed to variability in vessel performance. They emphasized the serious problems inherent in the standardization of results among different research vessels and proposed that special studies be undertaken to evaluate such errors but at the same time acknowledged the difficulty of carrying out such experiments. More recently, Koeller (1991) proposed approaches for improving survey abundance estimates by controlling trawl geometry. Another workshop featured attempts to analyze the differences and changes in the fishing power of the research vessels involved in the International Bottom Trawl Survey (IBTS) program in the North Sea (Anonymous 1992). Although sampling methods and fishing gears are a priori standardized in this survey program, catches were found to differ markedly among vessels, both qualitatively (in their species composition) and quantitatively. The workshop finally recommended that (*i*) "pairwise/parallel trawling should be incorporated in the allocation of vessels by area for multi-vessels surveys, permitting comparison of fishing power as data sets are accumulated over the years," and (*ii*) "whenever possible, the same vessel should be retained over time. Before old vessels are replaced by new ones, calibration studies should be undertaken." The need for intercalibration experiments between research vessels was thus acknowledged in multi-vessel survey programs and when survey vessels are replaced over time.

Received February 24, 1998. Accepted September 17, 1998. J14463

D. Pelletier. Laboratoire MAERHA, IFREMER BP 1105, 44311 Nantes Cedex 03, France.

© 1998 NRC Canada

Table 1. Survey designs for the intercalibration experiments realized from independent hauls.

Reference	Dates	Factorial design	Effective[a] no. of hauls	Survey area (s)
Sissenwine and Bowmann (1978)	1973–1975	2 vessels × 2 fishing gears × 2 day periods × 32 days × 2 replicates	515	one area of 65 km^2
Byrne and Forrester (1987)	1984	2 gears[b] × 4 day periods × 9 blocks × 4 replicates	288	9 blocks of 25 nmi^2
Ehrich (1991)	1986	3 gears–vessels × n[c] replicates	178	one area of 15×16 nmi^2
Ehrich et al. (1994)	1993	2 vessels × 2 areas × 25 replicates	79	2 areas of 100 nmi^2

[a]Some tows may not have been completed or may be invalid as the result of uncontrolled circumstances.
[b]The experiment used two research vessels, the differences in fishing power being accounted for in data analysis.
[c]n, not specified.

Table 2. Survey designs for the intercalibration experiments realized from paired hauls.

Reference	Dates	Station selection	No. of paired hauls[a]
Koeller and Smith (1983)	1978	Random	52
Fanning (1985)	1979	Random	94
	1980	Random	81
	1982	Random	49
Fanning (1984, 1985)	1983	Random	85 (72+13)[b]
Gavaris and Brodie (1984)	1983	High abundance	72
Byrne and Fogarty (1985)	1982	Stratified random	142
Byrne and Forrester (1991)	1981	Random	43
	1982	Random	140
	1986	Random	40
	1987	Random	83
	1988	Random	204
Warren (1996)	1995	Not specified	285

[a]Some tows may not have been completed or may be invalidated because of uncontrolled circumstances.
[b]With respect to the regular survey, 13 additional tows were achieved in zones of high abundance.

A number of intercalibration experiments have been carried out in the last two decades, mainly in North America and in Northern Europe. Results from these experiments highlight several points that need to be considered when conducting this type of study, namely the choice of sampling design, methods of gear monitoring, and approaches to data analysis.

Sampling design

Differences between vessel catchabilities may be obscured by the spatio-temporal variability of resource abundance and abiotic factors such as depth, substrate type, and hydrological and weather conditions. Intercalibration experiments should be designed to minimize these sources of variability. Two approaches have been used to compare vessels in the previous experiments. In the first approach (Table 1), two vessels towed independently in small areas that were assumed to be homogeneous with respect to fish abundance and environmental conditions. Spatial variability within each area was considered as residual, therefore, the smaller the areas, the more precise the estimates. In one experiment (Byrne and Forrester 1987), where several areas were sampled, the between-areas variability was handled using a randomized block design. Estimating the block-treatment interactions required a large number of hauls (Table 1). In any case, designs based on independent hauls could not account for all of the sources of variability, and a substantial fraction of spatial heterogeneities could possibly remain as residual variability, inflating catch variance and decreasing both the precision of conversion coefficient estimates and the power of statistical tests. In contrast, designs based on paired hauls (Table 2) considerably reduced the consequences of spatio-temporal variabilities because the two vessels towed simultaneously at the same speed and as closely as possible to one another with the distance generally ranging from 1/4 to 1 nautical mile (nmi). In the case of paired hauls, only spatial variation at scales smaller than the between-vessels distance would be included as residual variability.

A second question pertaining to sampling design is the selection of stations. When the intercalibration experiment is conducted at the same time as the regular survey, station location is dictated by the latter. If this is not the case, then stations should be selected so as to maximize catch for all species of interest because low and zero catches are less informative in estimating conversion coefficients. Fanning (1984, 1985), Byrne and Fogarty (1985), and Byrne and Forrester (1991) reported inconclusive results for some species because of a relatively low catch abundance: the effective sample size, i.e., the number of nonzero tows, was not sufficient to detect differences between vessels because of the lack of power of the tests used. In most of the cited experiments, the effective sample size did not allow estimation of age- or length-specific conversion coefficients. Sometimes, conversion coefficients could only be estimated for groups of species (Byrne and Forrester 1987). Also, Ehrich et al. (1994) reported that a substantial number of non-valid hauls could result from initial operational problems experienced when new vessels are used in the survey.

Gear monitoring

Changes in trawl geometry can drastically affect survey catch (Doubleday and Rivard 1981). Godø (1990) evaluated the consequences of changes in gear efficiency on the accuracy and precision of survey abundance estimates. Gear behaviour was carefully monitored by instrumentation during the trawl surveys conducted recently by the National Marine Fisheries Service (NMFS) on the west coast of the United States (D. Somerton, NMFS, 7600 Sand Point, Seattle, WA 98115, personal communication). Commercial vessels were

© 1998 NRC Canada

Table 3. Summary of statistical methods used to analyze the intercalibration data in the examples cited.

Reference	Data transformation	Statistical method	Treatment of zero catch
Sissenwine and Bowmann (1978)	Log catch	Linear model	sna
Byrne and Forrester (1987)	Log catch	Linear model	sna
Ehrich (1991)	Log catch for some species	Parametric and non-parametric tests	Included
Ehrich et al. (1994)	Not specified	Non-parametric tests	Included
Koeller and Smith (1983), Fanning (1984, 1985)	Catch index	Index modelled via a β-distribution	Handled through catch index
Gavaris and Brodie (1984)	Log catch	Linear model	Zeroes excluded
Byrne and Fogarty (1985)	None	Non-parametric tests	Included
Byrne and Forrester (1991)	Log catch	Paired *t*-tests	zpe
Warren (1996)	Log catch ratio	Linear model	zpe[a]

Note: sna, small number added; zpe, zero pairs excluded.
[a]Pairs with only one zero catch are handled using a mixed delta Poisson distribution.

chartered for these surveys, and monitoring of the gear was necessary to reduce at least the catch variability resulting from gear fluctuations and to standardize to some extent the catch among different vessels. Both Godø (1990) and Koeller (1991) state that real-time monitoring and stabilization of trawl geometry are more efficient than a posteriori standardization of catch using relationships between catch and gear parameters. In particular, catch per unit effort (CPUE) was found to be less sensitive to the variability of trawl geometry (vertical opening and wingspread distance) than abundance indices based on swept-area computations (Godø and Engås 1989).

Most of these studies emphasized the need for monitoring gear fluctuations by instrumentation so as to evaluate its impact on catch variability and to precisely determine effective haul duration. However, gear monitoring cannot account for crew effects or other vessel effects such as radiated noise, which has proved to be important for some species (Mitson 1992). These effects may be compared between vessels during an intercalibration experiment.

Data analysis

Koeller and Smith (1983) listed all of the potential problems posed by the estimation of conversion coefficients. They evaluated the effects of depth and towing distance and detected outliers through exploratory data analysis. In most of the previous experiments, the empirical distributions of the CPUE data were severely skewed with a high proportion of zero values. Zero observations were either excluded from the analysis or were retained in the analysis by adding a small number to them (Table 3).

Gear and (or) vessels effects were often estimated and tested using a multiplicative model (Robson 1966), i.e., a linear model applied to log-transformed data (Sissenwine and Bowmann 1978; Gavaris and Brodie 1984; Byrne and Forrester 1987, 1991) (Table 3). Ehrich (1991) only used log transformation for species for which empirical catch distributions were significantly skewed; for these species, vessel effects were then tested using Student's *t*-tests. Koeller and Smith (1983) and Fanning (1984, 1985) proposed a relative catch index that was less sensitive than the catch ratio to the skewness of catch distribution. Fanning (1984, 1985) modelled the distribution of this index using a β-distribution with parameters estimated from a least-squares fit. Alternatively, non-parametric estimation methods that require no assumption about data distribution were used by Byrne and Fogarty (1985), Ehrich (1991), and Ehrich et al. (1994).

The main fisheries research vessel (RV) of the French Institute for the Exploitation of the Sea (IFREMER), *Thalassa I*, was replaced in 1996 by a new vessel, *Thalassa*. It was necessary to maintain the temporal continuity of the time series of data for the annual trawl surveys conducted by IFREMER: the International Bottom Trawl Survey (IBTS) program in the North Sea and the EVHOE (Assessment of Fisheries Resources in Western Europe) program in the Celtic Sea. An intercalibration experiment based on paired hauls was conducted in 1996 to estimate conversion coefficients between vessels. In this paper, I present the estimation procedure developed for this experiment. In a second part, I show how the survey was planned using computer simulations and past survey data. Conversion coefficients are then estimated for the experimental data. The method is discussed in the last section.

Estimating conversion coefficients from a quasi-likelihood method

In light of the studies reviewed in the Introduction section, the statistical model chosen to estimate conversion should allow for skewed catch distributions and explicitly capture the existence of zero catches. Two estimation methods could be used in this respect: (*i*) parametric or semi-parametric approaches based on likelihood provided that either an appropriate distribution or at least some features of that distribution may be used; and (*ii*) approaches based on sampling theory that require few or no assumptions about data distribution (Cochran 1977). The latter lead to quite simple estimators that are appropriate for large data sets under a wide range of conditions for data distribution. A conversion coefficient may, for instance, be estimated from the ratio of mean catch, i.e., the total catch of one vessel in the area divided by the total catch of the other vessel in the same area. The information arising from paired hauls is not used in this approach because this approach assumes that for a given vessel, every tow within a sampling area is drawn from the same probability distribution; the spatial heterogeneity within the area is in fact neglected, thus increasing sampling variability.

On the other hand, we may assume that the two vessels sample a realization of the random function describing fish

© 1998 NRC Canada

abundance with this random function exhibiting spatial correlation. This kind of assumption may be handled through a quasi-likelihood estimation method. This is the approach followed here because it may explicitly capture quite general assumptions about the abundance process. In addition, likelihood-based methods enable one to study the theoretical properties of estimators, although these may be quite complex and may not be expressed under a closed form.

Quasi-likelihood approaches may be considered as a generalization of likelihood approaches in that they do not require a full specification of the distribution of the observations. It may be sufficient to assume, for example, a mean–variance relationship for the underlying random variable (Wedderburn 1974), with unknown parameters that could be estimated through the procedure. The statistical properties of quasi-likelihood functions are quite similar to those of likelihood functions, in particular for the distributions belonging to the exponential family such as binomial, Poisson, or Gaussian distributions. In addition, this approach may account for spatial heterogeneities of the abundance by specifying appropriate distributional characteristics. An aggregated distribution may for instance be represented through a mean–variance relationship. This is particularly interesting because, in general, building a probability model for discrete overdispersed observations is not a trivial task. Gauthiez (1994) has used quasi-likelihood functions to estimate fishing powers and abundance indices, as well as parameters of mean–variance relationships from CPUE data.

Assumptions and quasi-likelihood function

Let us assume that an experiment of paired hauls has been carried out to estimate conversion coefficients between two research vessels. For each species, paired catches (C_{1i}, C_{2i}) are available at a set of n stations indexed by i, subscripts 1 and 2 corresponding to the old and new research vessels, respectively.

The fish abundance sampled by a vessel at a given station is assumed to be the realization of a random variable. It is not necessary to suppose that the two vessels sample the realization of the same variable. Rather, it is assumed that the abundances N_{1i} and N_{2i} at a given station i are two random variables with same expectation, these random variables being spatially correlated so that

$$(1)\qquad \begin{aligned} E(N_{1i}) &= E(N_{2i}) \\ \mathrm{Cor}(N_{1i}, N_{2i}) &= \rho \end{aligned}$$

At a given station i, research vessel 1 (RV1) and research vessel 2 (RV2) sample a realization of N_{1i} and N_{2i}, respectively. Although vessels tow as closely as possible to one another, it is assumed that there is no interaction between their fishing operations, i.e., their catches at a given station are conditionally independent. Every fish has the same probability of being caught. The conversion coefficient x between the catch of both vessels is defined so that the catch of the old research vessel (RV1) is standardized with respect to the new one (RV2). Hence, the expected values of the catches C_{1i} and C_{2i} at a given station i are denoted

$$(2)\qquad \begin{aligned} \mu_{1i} &= E(C_{1i}) = \theta_i = q_1 E(N_{1i}) \\ \mu_{2i} &= E(C_{2i}) = x\theta_i \end{aligned}$$

where q_1 is the catchability coefficient relative to RV1 for the species of interest. Hence, x is a proportionality coefficient between the catchabilities of the two vessels.

At a given station i, the quasi-likelihood function K_i $(C_{1i}, C_{2i}, \boldsymbol{\Theta}_i)$ (Wedderburn 1974) is defined as

$$(3)\qquad \frac{\partial K_i}{\partial \boldsymbol{\Theta}_i} = \frac{\partial' \mathbf{M}_i}{\partial \boldsymbol{\Theta}_i} V^{-1}(\boldsymbol{\Theta}_i) \begin{pmatrix} C_{1i} - \theta_i \\ C_{2i} - x\theta_i \end{pmatrix}$$

where $\mathbf{M}_i = \begin{pmatrix} \mu_{1i} \\ \mu_{2i} \end{pmatrix}$, $\boldsymbol{\Theta}_i = \begin{pmatrix} x \\ \theta_i \end{pmatrix}$, and $\mathbf{V}(\boldsymbol{\Theta}_i)$ is the covariance matrix of catches that depends on parameters $\boldsymbol{\Theta}_i$:

$$(4)\qquad \mathbf{V}(\boldsymbol{\Theta}_i) = \begin{bmatrix} V(C_{1i}) & \mathrm{Cov}(C_{1i}, C_{2i}) \\ \mathrm{Cov}(C_{1i}, C_{2i}) & V(C_{2i}) \end{bmatrix}$$

Parameter estimates are obtained by solving the equation system

$$(5)\qquad \sum_{i=1}^{n} \frac{\partial K_i}{\partial \boldsymbol{\Theta}_i} \equiv 0,$$

where the sum is taken over the n stations. Solving this equation system requires the covariance matrix of catches $\mathbf{V}(\boldsymbol{\Theta}_i)$ at each station i.

Covariance matrix of catches

Following the classical expression of a conditional variance (Bickel and Doksum (1977), p. 36), the elements of $\mathbf{V}(\boldsymbol{\Theta}_i)$ in eq. 4 are written

$$(6)\qquad \begin{aligned} V(C_{1i}) &= V_{Ni}(E(C_{1i}|N_{1i})) + E_{Ni}(V(C_{1i}|N_{1i})) \\ V(C_{2i}) &= V_{Ni}(E(C_{2i}|N_{2i})) + E_{Ni}(V(C_{2i}|N_{2i})) \\ \mathrm{Cov}(C_{1i}, C_{2i}) &= \mathrm{Cov}_{Ni}(E(C_{1i}|N_{1i}), E(C_{2i}|N_{2i})) \\ &\quad + E_{Ni}(\mathrm{Cov}(C_{1i}|N_{1i}, C_{2i}|N_{2i})) \end{aligned}$$

The subscript Ni merely means that either the variance or the expectation is to be taken over the distribution of the random variable for abundance.

In each expression of eq. 6, the first term pertains to the variance structure of the underlying abundance because it expresses the variance relative to the abundance process. This term accounts for the paired nature of hauls. The second term pertains to sampling variability. Note that formulating these variances as a function of the parameters does not require a full specification of the abundance distribution, a mean–variance relationship, for instance, being sufficient.

Interestingly, a mean–variance relationship is a possible way of representing aggregated spatial distributions. Taylor (1961) suggested that the empirical variance and the empirical mean of animal populations may be related through a power function that is independent of the distribution of the population. The coefficient of the power function was considered as indicative of the rate of change of the spatial behaviour of an animal in response to a change in population density. This relationship has been empirically observed in many instances (e.g., see Downing (1986) for an application to marine organisms). Most frequently, variance was found to be a quadratic function of the mean (Perry 1981; Gauthiez

© 1998 NRC Canada

Table 4. Species caught during the IBTS and EVHOE surveys with associated Rubbin code.

Rubbin code	Scientific name	Common name	Rubbin code	Scientific name	Common name
AGON CAT	*Agonus cataphractus*	Hooknose	MELA AEG	*Melanogrammus aeglefinus*	Haddock
ARGE SIL	*Argentina silus*	Greater argentine			
ARGE SPH	*Argentina sphyraena*	Smaller argentine	MERL MCC	*Merluccius merluccius*	European hake
ARNO IMP	*Arnoglossus imperialis*	Scaldfish	MERL MNG	*Merlangius merlangus*	Whiting
ASPI CUC	*Aspitrigla cuculus*	Red gurnard	MICR KIT	*Microstomus kitt*	Lemon sole
BUGL LUT	*Buglossidium luteum*	Solenette	MICR POU	*Micromesistius poutassou*	Blue whiting
CALL LYR	*Callionymus lyra*	Dragonet			
CALL MAC	*Callionymus maculatus*	Spotted dragonet	MICR VAR	*Microchirus variegatus*	Thickback sole
CAPR APE	*Capros aper*	Boarfish	MOLV MOL	*Molva molva*	Ling
CLUP HAR	*Clupea harengus*	Atlantic herring	MULL SUR	*Mullus surmuletus*	Striped red mullet
CONG CON	*Conger conger*	European conger	MUST AST	*Mustelus asterias*	Starry smoothhound
ECHI VIP	*Echiichthys vipera*	Lesser weever	NEPH NOR	*Nephrops norvegicus*	Nephrops
ENCH CIM	*Enchelyopus cimbrius*	Four-bearded rockling	PHYC BLE	*Phycis blennoides*	Greater fork-beard
EUTR GUR	*Eutrigla gurnardus*	Grey gurnard	PLAT FLE	*Platichthys flesus*	Flounder
GADI ARG	*Gadiculus argenteus*	Silvery pout	PLEU PLA	*Pleuronectes platessa*	Plaice
GADU MOR	*Gadus morhua*	Cod	RAJA BAI	*Raja batis*	Grey skate
GAID VUL	*Gaidropsarus vulgaris*	Three-bearded rockling	RAJA CLA	*Raja clavata*	Roker
GLYP CYN	*Glyptocephalus cynoglossus*	Witch	RAJA FUL	*Raja fullonica*	Shagreen ray
			RAJA MON	*Raja montagui*	Spotted ray
GOBI NIG	*Gobius niger*	Black goby	RAJA NAE	*Raja naevus*	Cuckoo ray
HELI DAC	*Helicolenus dactylopterus*	Red bream	RAJA RAI	*Raja radiata*	Starry skate
			SALM SAL	*Salmo salar*	Atlantic salmon
HIPP PLA	*Hippoglossoides platessoides*	Long rough dab	SCOM SCO	*Scomber scombrus*	Atlantic mackerel
			SCYL CAN	*Scyliorhinus canicula*	Dogfish
HYPE LAN	*Hyperoplus lanceolatus*	Greater sandeel	SOLE VUL	*Solea vulgaris*	Common sole
ILLE COI	*Illex coindetii*	Broadtail shortfin squid	SPRA SPR	*Sprattus sprattus*	Sprat
			SQUA ACA	*Squalus acanthias*	Picked dogfish
LEPI WHI	*Lepidorhombus whiffiagonis*	Megrim	TRAC TRU	*Trachurus trachurus*	Horse mackerel
			TRIG LUC	*Trigla lucerna*	Tub gurnard
LIMA LIM	*Limanda limanda*	Dab	TRIS ESM	*Trisopterus esmarki*	Norway pout
LOLI FOR	*Loligo forbesii*	Common squid	TRIS LUS	*Trisopterus luscus*	Pouting
LOPH BUD	*Lophius budegassa*	Monkfish	TRIS MIN	*Trisopterus minutus*	Poor cod
LOPH PIS	*Lophius piscatorius*	Monkfish	ZEUS FAB	*Zeus faber*	John Dory
LUMP LAM	*Lumpenus lampretaeformis*	Snake blenny			

1994). Henceforth, N_{1i} and N_{2i} are assumed to follow a quadratic mean–variance relationship:

$$V(N) = \alpha E(N)^2 \tag{7}$$

The second term in eq. 6 pertains to the sampling variability and is tied to the conditional variance of catches. Catches are assumed to be conditionally independent and distributed as a Poisson process. Together with eqs. 1 and 7, this leads to the following expression for $\mathbf{V}(\mathbf{\Theta}_i)$:

$$\mathbf{V}(\mathbf{\Theta}_i) = \begin{bmatrix} \alpha\theta_i^2 + \theta_i & x\rho\alpha\theta_i^2 \\ x\rho\alpha\theta_i^2 & x\theta_i(1 + \alpha x\theta_i) \end{bmatrix} \tag{8}$$

Parameter estimators

The quasi-likelihood equation is finally obtained from eq. 3 after replacing $\mathbf{V}(\mathbf{\Theta}_i)$ and $\frac{\partial^t \mathbf{M}_i}{\partial \mathbf{\Theta}_i}$ to yield

$$\sum_{i=1}^{n} \begin{bmatrix} 0 & \theta_i \\ 1 & x \end{bmatrix} \begin{bmatrix} \alpha\theta_i^2 + \theta_i & x\rho\alpha\theta_i^2 \\ x\rho\alpha\theta_i^2 & x\theta_i(1 + \alpha x\theta_i) \end{bmatrix}^{-1} \times \begin{pmatrix} C_{1i} - \theta_i \\ C_{2i} - x\theta_i \end{pmatrix} = 0 \tag{9}$$

To simplify the solution of eq. 9, the abundances sampled by both vessels are assumed to have a common and constant expectation θ. This might be a reasonable assumption if the experiment is carried out in as small an area as possible because the heterogeneity of fish abundance within the area is then minimized. Such an assumption considerably decreases the number of parameters to estimate and makes them simpler to express. Under these conditions, there are two solutions to eq. 9, one of which should be ruled out because it leads to negative or nondefinite values for $\hat{\theta}$ whatever the value of ρ between –1 and 1. The other solution is

$$\begin{aligned} \hat{x} &= C_{2T}/C_{1T} \\ \hat{\theta} &= C_{2T}/n \end{aligned} \tag{10}$$

© 1998 NRC Canada

Table 5. RMSE of the estimates obtained from the simulations for each species in each potential sampling zone in the North Sea.

Potential sampling zone	CLUP HAR 1	SPRA SPR 1	GADU MOR 1	MERL MNG 1	MELA AEG 1	TRIS ESM 1	SCOM SCO 1	TRIS MIN 2	TRIS LUS 2	CALL LYR 2	LIMA LIM 2	PLEU PLA 2	SOLE VUL 2	MICR KIT 2
1	7	2	3	2	10	na	na	1	1	2	4	9	2	na
2	na	1	9	2	na	na	na	1	1	2	6	9	1	na
3	7	1	4	2	na	na	na	na	2	10	4	na	na	3
4	10	1	na	3	na	na	na	9	na	na	7	5	1	na
5	na	2	8	2	na	na	na	3	na	2	5	na	na	1
6	3	3	3	1	na	10	na	9	na	na	5	9	3	1
7	1	1	4	1	na	na	na	4	na	na	1	5	na	na
8	1	1	na	1	na	na	na	7	na	na	3	5	na	na
9	1	1	5	1	na	na	na	na	na	na	1	3	na	na
10	3	5	1	1	1	1	na	1	1	1	1	3	na	1
11	1	2	1	1	1	1	10	3	3	2	2	3	na	3
12	1	2	2	1	1	1	na	2	na	na	2	4	na	na
13	1	na	1	1	1	1	na	3	na	na	6	1	na	1
14	2	2	1	1	1	1	na	3	10	1	2	5	na	3
15	1	5	1	1	1	1	na	2	na	1	4	9	na	1
16	2	4	4	1	2	1	na	9	na	3	7	9	na	na
17	1	4	2	1	1	1	na	2	na	na	5	1	na	2
18	1	na	2	1	1	1	2	2	na	na	4	1	na	na
19	8	8	8	3	na	na	na	na	na	na	1	8	na	na
20	na	4	8	4	na	na	na	na	na	na	2	10	na	na
21	1	1	6	1	2	na	na	4	3	2	3	5	na	na
22	2	5	2	1	na	3	na	3	1	na	4	5	na	na
23	1	1	na	5	na	na	na	na	na	na	1	3	na	na
24	1	1	5	4	na	na	na	na	3	1	1	3	na	na
25	1	1	na	5	na	na	na	na	na	na	1	3	2	na
26	1	1	4	6	na	na	na	na	na	2	2	2	na	na
27	1	1	3	3	na	na	na	9	na	na	2	6	na	1
28	1	2	10	6	na	na	na	na	4	na	3	5	na	na
29	1	1	4	4	na	na	na	na	2	na	1	4	na	na
30	1	1	3	3	na	na	na	na	na	na	1	3	2	na
31	1	6	3	6	na	na	na	na	na	na	1	2	na	na
32	1	5	4	3	na	na	10	10	na	na	2	2	na	na
33	1	5	3	6	na	na	na	na	na	na	1	2	3	na
34	1	8	2	4	na	na	na	na	na	na	3	2	na	na
35	2	na	4	10	4	10	na	na	na	2	2	3	2	na
36	2	na	2	4	2	na	na	10	na	1	3	3	1	na
37	1	10	1	3	na	na	na	na	na	na	1	3	na	2
38	1	2	3	8	na	na	na	na	na	3	1	2	na	3
39	1	3	4	7	na	na	na	na	na	3	1	3	na	na
40	1	2	4	5	na	na	na	na	na	na	1	4	na	3
41	1	1	10	4	na	na	na	na	na	1	1	2	na	10
42	1	2	5	4	na	na	10	na	na	3	1	2	3	na
43	1	1	7	2	na	na	na	10	3	1	1	2	na	na
44	1	3	3	1	na	na	na	na	2	na	2	2	na	na
45	3	2	na	3	na	na	na	10	na	na	3	5	na	na
46	3	1	na	3	na	na	na	na	na	na	3	6	na	na
47	1	1	10	3	na	na	na	na	na	na	3	6	na	na
48	1	1	5	2	na	na	na	10	na	2	1	2	10	na
49	1	2	na	2	na	na	na	6	na	3	2	2	na	na
50	1	1	3	2	na	na	na	na	na	na	4	5	na	na
51	1	1	1	4	na	na	na	na	1	na	4	5	na	na
52	1	2	na	2	na	na	na	na	na	na	10	5	2	na
53	1	3	na	1	na	na	1	3	na	na	4	4	na	10
54	1	1	1	1	na	na	na	1	1	na	10	na	na	1

Note: Species priority is indicated below each species code; only species of high priority are reported. Each potential sampling zone corresponds to a station recently surveyed. The RMSEs (relative root mean square errors) were coded in 10 ordered classes, 1 being the best quality of estimation. The worst quality of estimation is "na" (not available), meaning that the conversion coefficient could not be estimated.

© 1998 NRC Canada

Table 6. RMSE of the estimates obtained from the simulations for each species in each potential sampling zone in the Celtic Sea.

Potential sampling zone	MERL MNG 1	MERL MCC 1	ASPI CUC 1	LEPI WHI 1	LOPH BUD 1	LOPH PIS 1	NEPH NOR 1	RAJA NAE 1	LOLI FOR 2	ILLE COI 2	SCYL CAN 2	ARGE SIL 2
1	1	1	3	2	na	na	na	na	9	7	1	1
2	1	2	2	1	1	na	na	na	8	6	1	na
3	na	2	na	1	na	1	na	na	na	3	1	na
4	1	1	2	4	na	na	1	na	6	2	2	1
5	na	1	na	1	na	na	na	na	na	2	na	1
6	2	2	na	1	na	na	2	na	na	2	1	1
7	1	2	2	1	na	1	na	na	na	1	2	1
8	1	1	na	2	1	na	na	na	3	5	1	na
9	na	2	na	2	na	na	na	na	na	1	na	1
10	1	1	2	3	1	na	na	na	na	1	na	1
11	na	1	3	1	na	na	na	1	na	3	1	na
12	1	1	10	5	na	2	10	na	4	3	2	na
13	1	1	na	9	na	na	1	na	6	3	1	na
14	10	4	na	4	na	na	2	na	na	2	na	1
15	1	1	na	2	na	na	na	na	na	3	2	1
16	na	1	na	5	na	na	1	10	na	6	1	na
17	na	1	na	6	1	na	1	na	2	9	1	na
18	1	1	2	4	1	na	10	na	4	10	1	na
19	na	1	3	1	na	na	na	1	na	4	1	1
20	na	1	na	1	1	na	na	1	na	3	1	na
21	10	2	2	2	na	1	na	na	na	na	1	na
22	2	1	1	2	na	na	na	na	6	2	1	1
23	2	2	na	1	na	na	10	2	na	2	1	1
24	2	3	1	3	na	na	na	na	2	na	2	1
25	na	1	na	na	na	na	2	na	8	2	1	1
26	2	2	10	2	na	na	na	na	na	7	1	na
27	na	2	2	1	na	2	na	1	10	na	1	1
28	na	1	na	1	na	na	3	10	na	2	2	1
29	na	1	na	1	2	na	1	na	na	2	na	1
30	2	1	2	2	na	1	na	na	na	3	1	1
31	1	1	na	3	na	na	2	na	5	na	2	1
32	na	na	na	na	na	2	1	na	na	3	na	1
33	na	1	1	1	na	na	na	1	5	5	1	1
34	na	2	na	2	na	na	na	na	na	2	na	1
35	na	10	na	na	na	2	na	na	na	9	na	1
36	na	1	2	2	na	na	na	1	2	4	1	na
37	2	2	1	1	na	10	na	2	1	na	1	10
38	na	1	na	4	na	na	na	na	na	7	2	1
39	na	1	2	2	na	1	na	2	10	4	1	1
40	1	1	1	2	na	na	na	2	1	v	1	1
41	na	1	na	2	2	1	na	na	na	3	10	1
42	na	1	na	4	10	na	na	na	na	3	1	2
43	na	2	1	1	na	na	na	1	3	9	1	v
44	na	2	1	1	na	1	na	2	3	10	1	na
45	na	2	1	1	1	1	10	1	4	1	1	1
46	na	2	na	1	1	1	na	na	na	3	2	na
47	2	1	1	1	1	na	na	na	na	5	2	1
48	2	2	1	3	na	na	2	1	1	9	1	1
49	2	2	1	1	na	na	na	na	7	3	1	1
50	3	2	1	5	1	na	na	1	3	7	na	1
51	na	1	1	3	na	na	10	na	1	4	1	na
52	2	3	1	4	na	na	10	1	3	3	1	na
53	na	4	1	2	2	na	na	1	1	1	1	na
54	na	3	1	5	na	na	na	1	1	4	1	1

© 1998 NRC Canada

ARGE SPH 2	GADU MOR 2	TRIS MIN 2	MICR POU 2	CAPR APE 2	TRAC TRU 2	GADI ARG 2	MICR VAR 2
4	5	1	4	na	na	na	na
1	1	9	na	5	1	na	na
na	9	2	3	2	1	na	na
2	na	2	3	na	na	na	na
6	3	1	1	1	1	1	1
1	8	1	5	2	na	na	1
1	5	1	na	9	2	na	na
1	6	1	1	9	na	na	
na	na	5	1	2	1	1	1
2	1	1	10	6	na	na	na
2	na	7	3	1	1	na	1
2	7	1	1	10	na	na	na
1	5	1	1	na	na	na	na
na	na	na	3	4	na	1	1
1	2	6	na	3	1	na	na
4	na	1	1	10	3	na	na
3	2	1	1	5	10	na	na
1	5	1	2	na	na	na	na
na	na	7	1	1	1	na	1
1	na	na	4	1	1	na	1
1	2	1	2	na	na	na	na
3	2	1	na	na	1	na	10
1	na	1	na	2	1	na	na
1	10	1	3	4	na	na	10
na	na	1	1	4	1	na	2
7	4	2	na	9	1	na	na
1	2	1	3	5	1	na	na
3	na	6	10	3	1	na	na
na	9	8	1	1	1	1	1
2	na	1	1	1	1	1	1
2	1	1	1	6	na	10	na
na	na	na	4	na	na	na	na
2	5	3	2	2	1	na	1
na	na	na	2	4	na	1	1
na	na	na	na	na	na	na	na
2	2	1	3	na	1	na	na
7	7	1	1	na	1	na	na
1	8	1	2	1	1	na	1
1	9	1	1	1	1	na	na
1	4	1	1	2	2	na	na
2	na	2	1	1	1	2	1
7	7	5	1	6	1	na	10
na	3	1	na	3	1	10	2
10	9	10	na	1	1	na	na
1	10	2	3	1	1	na	na
9	9	na	1	1	1	na	1
1	na	10	7	1	1	na	1
2	5	1	1	2	1	na	2
1	na	na	4	1	1	na	2
2	9	1	1	3	3	na	na
2	9	3	3	3	1	na	na
5	na	1	1	1	1	na	na
6	9	1	7	1	1	na	na
2	9	1	3	1	1	na	na

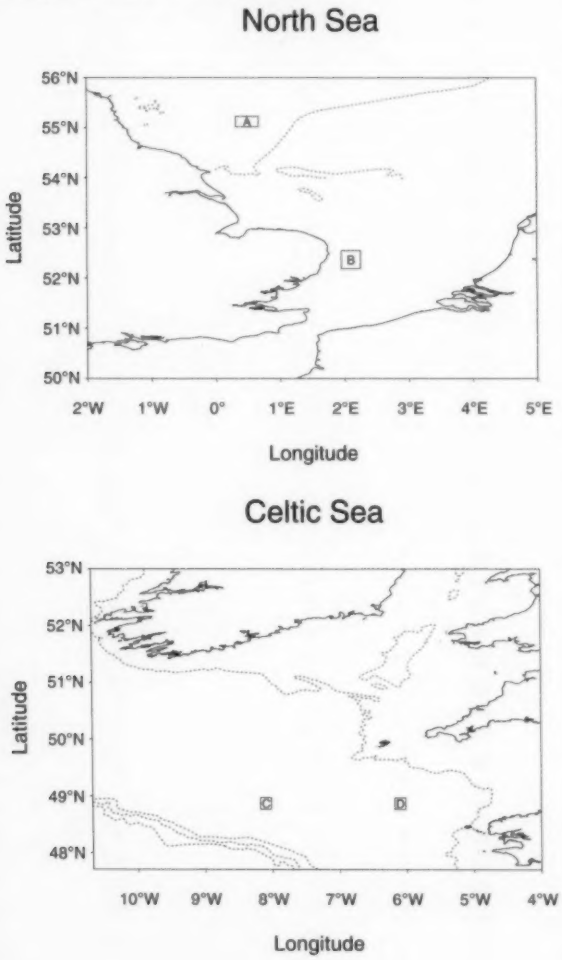
© 1998 NRC Canada

Table 6 (*concluded*).

Potential sampling zone	MERL MNG 1	MERL MCC 1	ASPI CUC 1	LEPI WHI 1	LOPH BUD 1	LOPH PIS 1	NEPH NOR 1	RAJA NAE 1	LOLI FOR 2	ILLE COI 2	SCYL CAN 2	ARGE SIL 2
55	na	10	1	2	na	1	na	1	2	2	1	1
56	1	2	1	10	na	na	na	1	1	6	1	na
57	na	4	1	2	na	1	na	1	5	4	1	2

Note: Species priority is indicated below each species code; only species of high priority are reported. Each potential sampling zone corresponds to a station recently surveyed. RMSEs (relative root mean square errors) were coded in 10 ordered classes, 1 being the best quality of estimation. The worst quality of estimation is "na" (not available), meaning that the conversion coefficient could not be estimated.

Fig. 1. Sampling zones of the INTERCAL survey. Each square corresponds to a 15 × 15 nmi^2 area.



where C_{1T} and C_{2T} denote total catch of RV1 and RV2, respectively.

These estimators are similar to those that could be obtained from a likelihood approach with a Poisson catch process, but their variances are different. Note that under the assumption of a common and constant expectation for θ, they are also a solution of eq. 5, whatever the underlying abundance process and sampling process. They are thus valid under more general conditions. The other derivations are nevertheless needed to analytically derive estimators of α and ρ and the asymptotic covariance matrix of $\hat{\boldsymbol{\theta}}$ and corresponding estimators. These estimators will not be explicitely developed here for two reasons. First, this paper focuses on estimating conversion coefficients rather than θ, α, and ρ. Second, asymptotic variances are in theory only valid for large sample sizes. Corresponding estimators may thus yield unreliable results in the case of survey data because sample sizes are usually relatively small. Note also that the estimator of x is asymptotically consistent, but there may be a bias for limited sample sizes. One way to increase the robustness of the estimators and to evaluate their bias and variance is to use the bootstrap procedure (Efron 1982). In this paper, the coefficient of conversion, its relative root mean square error (RMSE), and a 90% confidence interval were estimated from a nonparametric bootstrap procedure (see Appendix).

Survey planning

As already mentioned, the survey design consists of paired hauls conducted in one or several areas of limited extent. Planning the survey implies selecting the sampling area(s) and associated sample size(s) so as to obtain the best possible estimates of conversion coefficients for the species of interest in each region. Beforehand, it should be stressed that the sampling scheme is subject to external constraints that restrict the range of alternatives for survey planning. Hence, vessel operating costs limit the total number of hauls to approximately 120 for a survey, i.e., ca. 60 per region to be surveyed (North Sea and Celtic Sea). Recall, for instance, that a minimum sample size of ca. 30 is required when comparing means through a t-test. As a first approximation, this might be the lower limit for the sample size in one area. Therefore, two alternative options are considered in a given region: either conducting 30 hauls in each of two areas or conducting 60 hauls in a single area. Sampling areas and sample size are determined from computer simulations.

Sample simulation

For a given simulation scheme, paired catches $\{C_{1k}, k = 1,..., n\}$ and $\{C_{2k}, k = 1,..., n\}$ are generated from independent Poisson distributions with parameters θ and $x\theta$, respectively (see eq. 2). One-hundred replicates are generated and $\hat{x}^*$ and associated RMSE$^*(\hat{x}^*)$ are computed from eqs. A1 and A2, $\hat{x}_{ref}$ being equal to x. This procedure is repeated for each species in each region (the North Sea and the Celtic Sea).

© 1998 NRC Canada

ARGE SPH 2	GADU MOR 2	TRIS MIN 2	MICR POU 2	CAPR APE 2	TRAC TRU 2	GADI ARG 2	MICR VAR 2
3	na	na	1	1	1	na	1
2	na	1	1	3	1	na	na
6	na	2	1	2	1	na	2

Table 7. Characteristics of survey data used for the calibration study.

Region	Zone	No. of valid paired hauls	No. of species in the catch	Dimensions in the zone (nmi)
North Sea	A	24	23	13 N–S per 12 E–W
North Sea	B	22	27	21 N–S per 11 E–W
Celtic Sea	C	30	37	13 N–S per 15 E–W

Each simulation scheme corresponds to a sampling scenario and a value of x. The values of x considered in the simulations range from 1 to 3 based on the assumption that the new vessel is likely more efficient at catching fish than the old one. Note that no assumption about parameters α and ρ needs to be made for simulations. Regarding sampling scenario, two sample sizes are considered, viz. 30 and 60 per area. In a given region, each potential sampling area corresponds to a small zone centered around each station that was sampled in the past during the regular surveys. Previous surveys provide the best a priori information about potential catch, i.e., about parameter θ. Because the intercalibration experiment was initially programmed in March 1996, the most recent survey data from the closest seasons were used, i.e., February 1994 for the North Sea and May 1991 for the Celtic Sea. In each survey, 49 and 64 species were caught at 54 and 57 stations, respectively (Table 4). Note that such simulations are conditional on the values of θ that can be inferred from the survey data: no variation of this parameter was considered for planning purposes.

Simulation outcomes

Similar results were obtained for all simulation schemes considered. In particular, the area(s) selected under a given scheme should also be appropriate for the range of values of x explored. This is interesting because x likely differs among species. As another consequence, results were only reported for one scheme ($x = 1$ and $n = 30$). To facilitate the interpretation of the results, the RMSEs were coded in 10 ordered classes, 1 being the best quality of estimation (Tables 5 and 6). The worst quality of estimation is "na" (not available), meaning that the conversion coefficient could not be estimated. Such cases occur when there is at least one bootstrap replicate with null catch over the sample for RV1, leading to an infinite or undefined value of $\hat{x}_b^*$. In practice, this means that the abundance observed at this station during the survey, i.e., the expected value of θ used for the simulations, was very low or even zero (the species was rare in or absent from the catch).

Table 8. Length limits used to build the length classes for length-based estimates of conversion coefficients.

Species	Zone	Length limit (cm)
CLUP HAR	A and B	15
GADU MOR	A and B	50
MERL MNG	A and B	15
SPRA SPR	A and B	12
HIPP PLA	A	15
TRIS ESM	A	12
AGON CAT	B	8
ARNO IMP	C	11
SCOM SCO	C	22
TRAC TRU	C	15

Past surveys indicated a substantial spatial variation of the species composition of catches within each region. This suggests the importance of considering two sampling areas rather than one in each region because it would be difficult to pick a single area that allows for a correct estimation of conversion coefficients for every species of interest. Simulation results confirmed this observation. Consequently, two areas were to be selected in each region, implying a sample size of 30 paired hauls in each. Fortunately, results were not qualitatively different according to sample size, and in addition, the estimation was not strikingly improved with a sample size of 60 hauls compared with 30 hauls.

For each region, selecting two areas had to rely on the examination of all results per species and station because these areas should be complementary with respect to species composition. Although it was desirable to have a conversion coefficient for each species, some species were more important than others because of their commercial value or their scientific interest. Species were prioritized by the scientists in charge of the survey programs following their own criteria (Tables 5 and 6). Low-priority species were not considered for planning purposes. Each station sampled in the past was regarded as a potential sampling area. The procedure for selecting two sampling areas was the following: the first area chosen exhibited a maximum number of species with best quality estimates (RMSE = 1) and the second area selected was the one with a maximum number of best quality estimates for the species that could not be estimated in the first area. Species priority was accounted for as far as possible. No automatic procedure was defined in this selection process. Within a given region, there were several areas that al-

© 1998 NRC Canada

lowed for similar qualities of estimation. For example, in the North Sea, stations 10–15 and 17 yielded good estimates for the most important species, except for mackerel (SCOM SCO) and sole (SOLE VUL) and to a lesser extent dragonet (CALL LYR) and pouting (TRIS LUS). Stations 1, 2, 35, and 36 appeared as complementary to stations 10–15 and 17 from this standpoint. In the Celtic Sea, the high number of species of interest made the choice less clear. Stations 45 and 48 a priori allowed for good estimates for many species of first and second priority. Stations 4 or 13 could complement them to estimate a coefficient for nephrops (NEPH NOR) and whiting (MERL MNG).

Of course, when selecting the areas, it was also necessary to keep in mind that 30 paired hauls should be safely carried out in these areas. A 15 × 15 nmi^2 area was thought an appropriate size. As quoted in a previous section, each sampling area should be as small as possible to limit the effects of spatial heterogeneity. Also, areas with hard substrate or those areas that may pose risks to the gear should be avoided. Lastly, the distance from the area to the port and the distance between sampling areas should be taken into account. Given these constraints, it was decided to define a first area (area A) in the North Sea around stations 12 and 14 and a second area (area B) around stations 1 and 2 (Fig. 1). In the Celtic Sea, the two respective areas (C and D) would be around stations 45 and 48. Thirty paired hauls would be conducted in each area.

Analysis of intercalibration data

Survey data

The intercalibration survey took place in October 1996 instead of March 1996 because of a delay in vessel construction. In addition, the survey design had to be adapted as the result of uncontrollable circumstances. The two areas planned in the North Sea (areas A and B) were sampled as expected, but only one area could be sampled in the Celtic Sea (area C) because of gear problems on the new vessel (Fig. 1).

In the analysis, a pair of hauls was considered valid if one vessel towed for the full 30 min and the other one towed for at least 20 min. The exact tow duration was measured by electronic sensors coupled with an automatic recording system (SCANMAR). If one vessel towed between 20 and 30 min, corresponding catch was rescaled to an equivalent 30-min tow. Other hauls were excluded from the analysis (see Table 7 for a summary of valid data). In each region, most species that were considered important for the routine survey (priority 1 in Tables 5 and 6) were found in a high proportion of paired hauls, with the exception of whiting and nephrops in the Celtic Sea. Some species were sometimes found to be very abundant in the catches. In the North Sea, catches in the two areas appeared to be complementary with respect to some species. Other species were found in both areas; therefore, a conversion coefficient could be estimated in each.

Although the estimation procedure allows for zero catch because of the statistical model used, it is obvious that a null catch for both vessels carries no information about the relative catchabilities of the vessels. The estimates of conversion coefficients will be more precise when (*i*) the species is present in a large number of hauls, (*ii*) the species catch is large, and (*iii*) the species is uniformly distributed over the sampled area. Therefore, species that exhibit many zero catches or small catches are likely to yield poor estimates of conversion coefficients. Examination of the data revealed frequent differences between the catches of the vessels for a given species at a given station; moreover, these differences were not always positive or negative within a given area, suggesting sampling variability. Note that according to model assumptions, possible aggregations at a scale smaller than the between-vessel distance were considered as sampling variability.

The length compositions of the data were also analyzed to examine particular features within an area. This was possible only for abundant species in the area where there were enough data to draw a histogram (Fig. 2). For most species, observed length structures were unimodal. However, some species exhibited two modes, e.g., cod (GADU MOR) and Norway pout (TRIS ESM) in area A (Fig. 2, zone A), hooknose (AGON CAT), whiting (MERL MNG), sprat (SPRAT SPR), horse mackerel (TRAC TRU), and poor cod (TRIS MIN) in area B (Fig. 2, zone B), and scaldfish (ARNO IMP), mackerel (SCOM SCO), and horse mackerel in area C (Fig. 2, zone C). In the North Sea, some species exhibited markedly different length compositions between area A and area B, say cod, herring (CLUP HAR), and whiting. For all these cases, conversion coefficients were estimated per length class. Because length compositions were found to be either unimodal or bimodal, two length classes were considered at most. The length limits of the two classes were determined from the length compositions (Table 8).

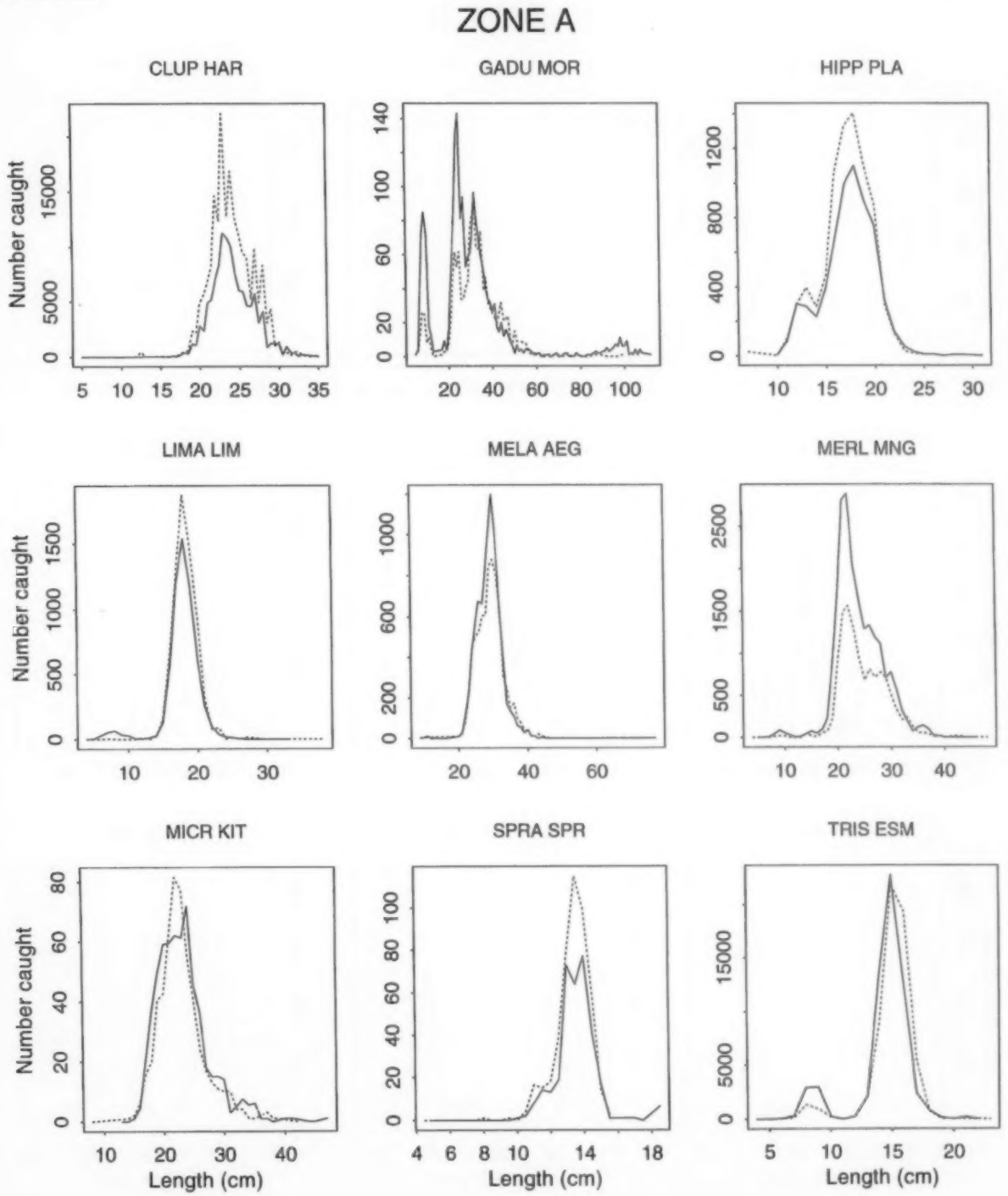
Conversion coefficient estimates

Bootstrap estimates $\hat{x}^*$ and $\mathrm{RMSE}^*(\hat{x}^*)$ of the conversion coefficients were computed from eq. A1 based on 1000 bootstrap replicates of the intercalibration data. The reference estimate $\hat{x}_{\mathrm{ref}}$ in eq. A1 was computed from the intercalibration data using eq. 10. Nonparametric confidence intervals (90%) were also computed. Note that only species with at least one nonzero haul in the area are considered in the estimation procedure, i.e., at least one vessel caught that species once in the area. Still, it may happen that in a bootstrap replicate b, the catch of one vessel is null over the whole area, leading to a zero or infinite value for $\hat{x}^*_b$. The probability of such a replicate may be computed from the real data. Experience has shown that this probability is nonnegligible only for species found in a small number of hauls within an area. If more than 1% of replicates result in zero or infinite values of $\hat{x}^*_b$, then the results for that species are discarded. Otherwise, the non-zero (non-infinity) results were retained for further analysis.

Length-based estimates are presented together with the other estimates. Estimates of good quality were arbitrarily selected as corresponding to confidence intervals no wider than 1 (Tables 9 and 10 and Fig. 3). The other estimates, i.e., with a confidence interval wider than 1, were considered of poorer quality (Table 11). For some species, data were available but reliable estimates could not be obtained because of too many low and null catches (Table 12). In the North Sea, when an estimate was available in each area, only the one with the smallest RMSE was retained.

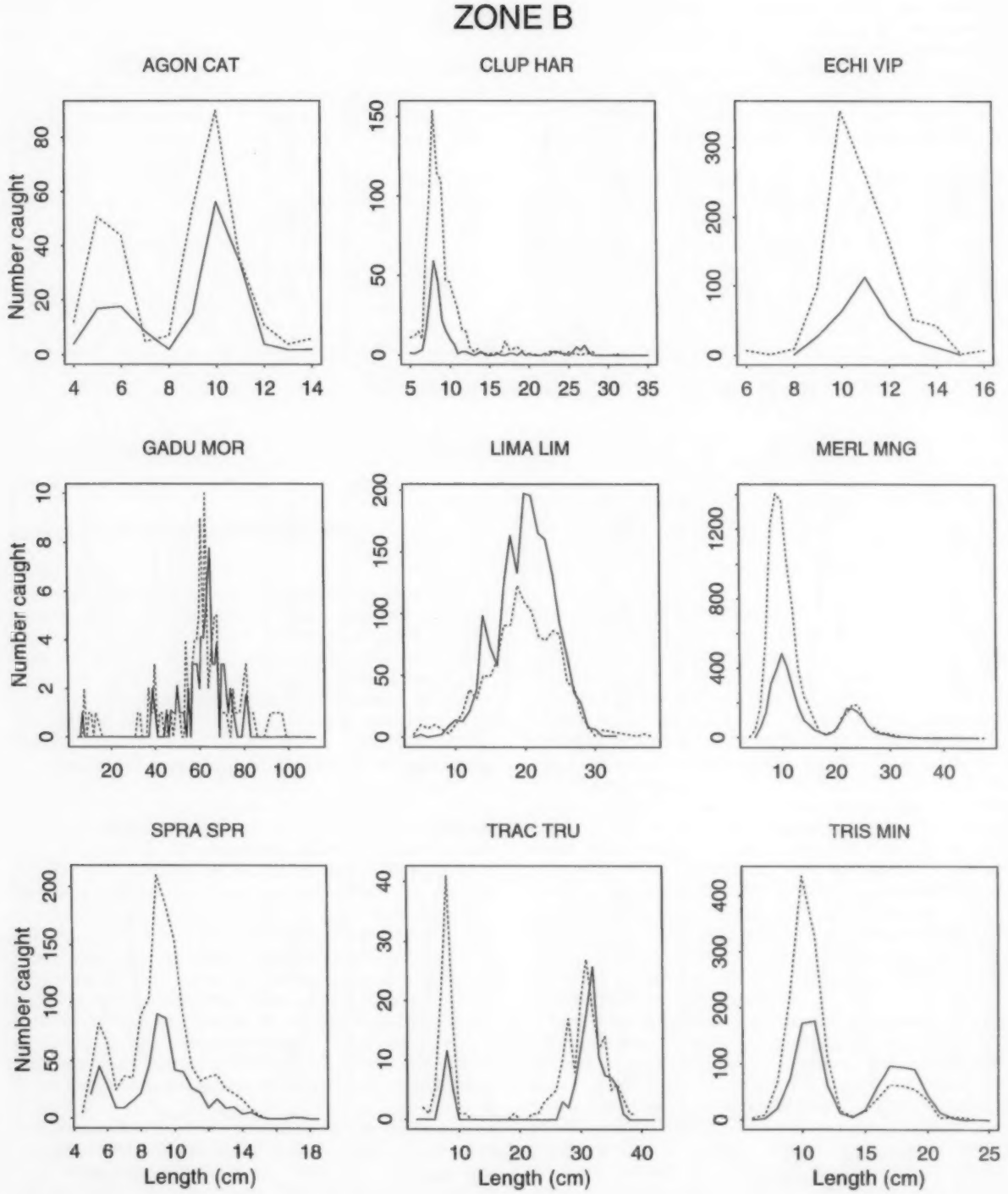
© 1998 NRC Canada

Fig. 2. Length compositions observed for the species that were most frequently found in the catch of a zone. Each distribution is calculated over the hauls of a given zone (zones A, B, and C). Catch is standardized to a 30-min haul. The catch distributions of the RV1 and RV2 are indicated with a solid and dotted line, respectively. See Table 4 for the correspondence between Rubbin code and species name.



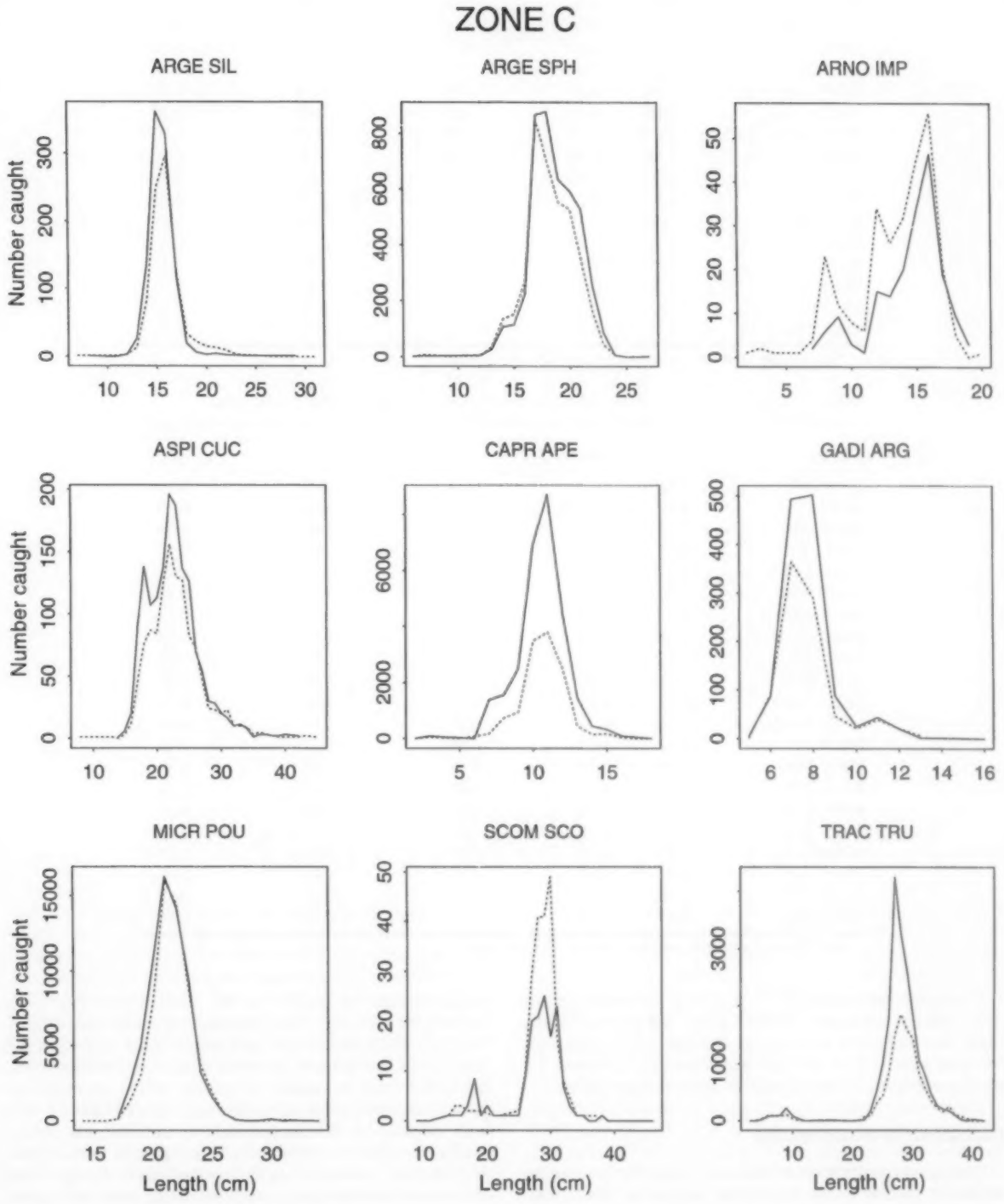
© 1998 NRC Canada

Fig. 2 (*continued*).



© 1998 NRC Canada

Fig. 2 (*concluded*).



© 1998 NRC Canada

Table 9. Species for which good quality estimates were obtained from North Sea data.

Species	$\hat{x}^*$	RMSE$^*(\hat{x}^*)$	Lower bound of CI	Upper bound of CI	Width of CI
EUTR GUR	0.64	0.24	0.43	0.92	0.49
GADU MOR ≤ 50	0.71	0.24	0.47	0.99	0.53
GADU MOR > 50	1.19	0.23	0.78	1.66	0.88
HIPP PLA	1.26	0.12	1.01	1.50	0.49
LIMA LIM > 15	1.24	0.24	0.87	1.78	0.92
MELA AEG	0.89	0.06	0.81	0.99	0.19
MERL MNG ≤ 15	0.29	0.52	0.06	0.55	0.50
MERL MNG > 15	1.15	0.10	0.98	1.34	0.36
MICR KIT	0.92	0.10	0.78	1.07	0.29
PLEU PLA	0.52	0.27	0.32	0.76	0.44
RAJA MON	1.06	0.31	0.62	1.65	1.03
RAJA RAI	1.24	0.20	0.89	1.67	0.78
SCYL CAN	0.79	0.55	0.35	1.40	1.04
SOLE VUL	1.50	0.16	1.12	1.86	0.74
TRIS ESM ≤ 12	0.43	0.26	0.27	0.61	0.34
TRIS ESM > 12	1.12	0.30	0.61	1.69	1.07

Note: Results for a 90% confidence interval (CI) are reported.

Table 10. Species for which good quality estimates were obtained from Celtic Sea data.

Species	$\hat{x}^*$	RMSE$^*(\hat{x}^*)$	Lower bound of CI	Upper bound of CI	Width of CI
ARGE SIL	0.89	0.24	0.61	1.27	0.66
ARGE SPH	0.88	0.11	0.73	1.04	0.30
ARNO IMP	1.55	0.13	1.26	1.90	0.64
ASPI CUC	0.78	0.09	0.66	0.89	0.22
CALL LYR	0.77	0.30	0.47	1.18	0.71
CAPR APE	0.53	0.68	0.22	1.18	0.97
GADI ARG	0.72	0.20	0.51	0.95	0.43
GADU MOR	1.00	0.31	0.61	1.50	0.89
ILLE COI	0.52	0.33	0.27	0.81	0.53
LEPI WHI	0.73	0.08	0.64	0.84	0.19
MELA AEG	0.79	0.21	0.57	1.09	0.52
MERL MCC	1.26	0.15	0.97	1.57	0.60
MICR KIT	0.51	0.23	0.38	0.67	0.28
MICR POU	0.90	0.11	0.74	1.07	0.33
RAJA FUL	0.60	0.44	0.30	1.06	0.76
RAJA NAE	0.53	0.12	0.43	0.64	0.20
SCYL CAN	1.43	0.17	1.09	1.85	0.76
SCOM ≤ 22	0.76	0.43	0.24	1.29	1.05
TRAC TRU ≤ 15	0.81	0.59	0.35	1.31	0.96
TRAC TRU > 15	0.59	0.28	0.36	0.88	0.52
TRIS MIN	0.65	0.12	0.52	0.78	0.26

Note: Results for a 90% confidence interval (CI) are reported.

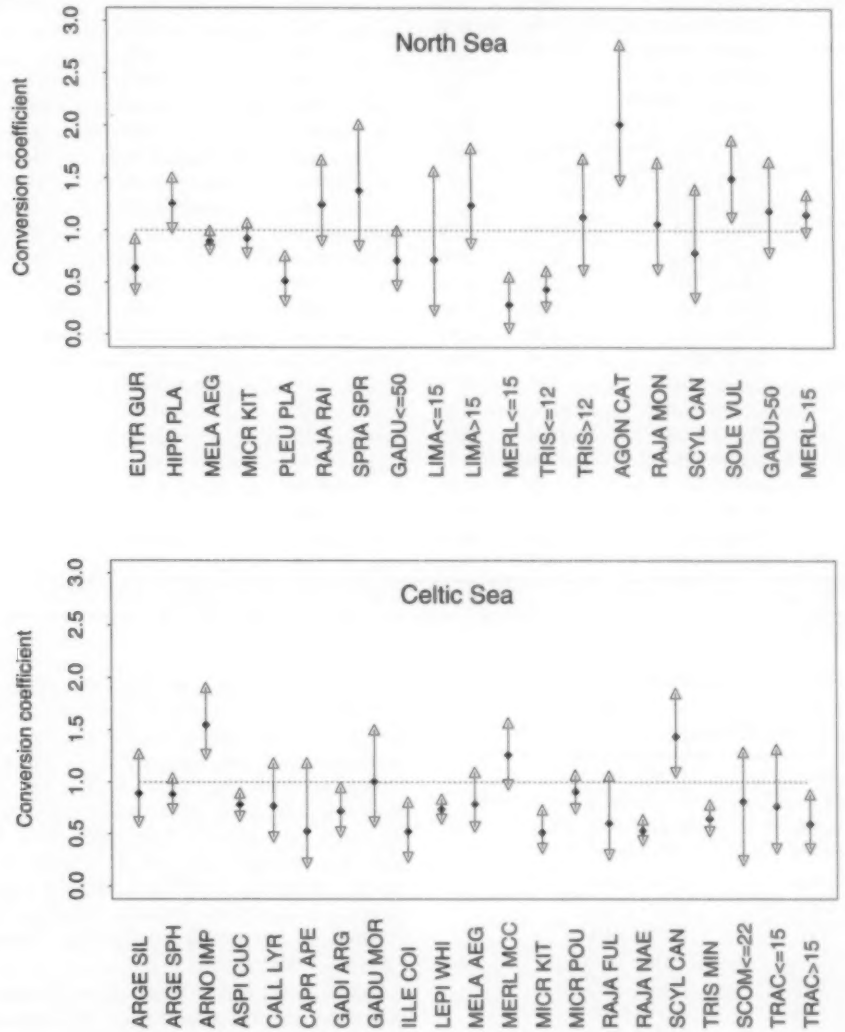
A length-based estimate was found to be necessary for cod, whiting, mackerel, Norway pout, and capelin in the North Sea and horse mackerel in the Celtic Sea. Estimates for sprat were similar for both length classes. Estimates for small mackerel and large scaldfish were of poor quality.

Discussion–conclusion

Conversion coefficients could be estimated for most of the important species in the North Sea and in the Celtic Sea, with the exception of whiting and nephrops, which were not caught during the survey in the latter region. For some species, the estimates were considered quite reliable (in particular haddock, lemon sole, and plaice in the North Sea and lemon sole, red gurnard, megrim, cuckoo ray, and others in the Celtic Sea). A number of species exhibit more or less poorer estimates, some of which could nevertheless be used with caution. No reliable estimate is available for the remaining species, or for whiting and nephrops in the Celtic Sea. In some cases, this is due to the season during which the intercalibration survey was conducted; only one experiment could be achieved, thus a time of the year had to be

© 1998 NRC Canada

Fig. 3. Confidence intervals (90%) obtained for species with good quality estimates (see Tables 9 and 10). For the North Sea (top), TRIS, MERL, LIMA, GADU refer to TRIS ESM, MERL MNG, LIMA LIM, and GADU MOR, respectively. For the Celtic Sea (bottom), SCOM and TRAC refer to SCOM SCO and TRAC TRU, respectively. See Table 4 for the correspondence between Rubbin code and species name.



chosen, during which some species may or may not be caught, depending on the region. Among species with good quality estimates, approximately half of the conversion coefficients can be considered as significantly different from 1 at a 90% confidence level. Thus, vessel catchabilities appear to be distinct with respect to many species. The interpretation of the values obtained in relation to species behaviour and vessel characteristics falls beyond the scope of this paper.

Estimates are in general of better quality in the Celtic Sea. The less satisfying results are obtained in the area B in the North Sea. This is probably linked with a relatively small sample size. Recall that 30 hauls were initially planned in each area and that this was only achieved in the Celtic Sea area. The sampling size that was planned from the simulations appears to have been appropriate here.

The estimated conversion coefficients may be used to standardize the catch of the old vessel with respect to the new one so that data obtained from past surveys are consistent with those obtained from surveys conducted with the new vessel. Catch data from the old vessel (RV1) should thus be converted as follows:

$$\hat{C}_l^{\text{new}} = \hat{x}\hat{C}_l^{\text{old}},$$

where $\hat{C}_l^{\text{old}}$ is the actual old vessel catch and $\hat{C}_l^{\text{new}}$ is the corresponding converted value. The uncertainty associated with $\hat{C}_l^{\text{new}}$ may be easily deduced from the variances or RMSEs of $\hat{x}$ and $\hat{C}_l^{\text{old}}$ because these were estimated from independent surveys. The conversion should only concern species for which the conversion coefficient was found to be significantly different from 1.

© 1998 NRC Canada

Table 11. Species for which poor quality estimates were obtained.

Region	Species	$\hat{x}^*$	RMSE$^*(\hat{x}^*)$	Lower bound of CI	Upper bound of CI	Width of CI
North Sea	AGON CAT	2.01	0.22	1.48	2.78	1.30
	CLUP HAR ≤ 15	3.76	0.36	2.13	6.05	3.92
	CLUP HAR > 15	1.45	0.37	0.68	2.33	1.65
	ECHI VIP	3.41	0.22	2.14	4.67	2.53
	HYPE LAM	9.53	0.43	5.05	15.86	10.80
	LIMA LIM ≤ 15	0.72	0.93	0.23	1.56	1.34
	LOPH PIS	1.08	0.96	0.33	2.50	2.17
	RAJA CLA	1.48	0.37	0.81	2.26	1.45
	SCOM SCO	2.10	0.72	0.57	4.57	4.00
	SPRA SPR	1.38	0.26	0.85	2.01	1.16
	SQUA ACA*	1.33	0.94	0.40	3.00	2.60
	TRAC TRU	2.12	0.36	1.09	3.39	2.30
	TRIG LUC	1.83	0.62	0.79	3.41	2.62
	TRIS LUS	1.99	0.47	0.92	3.55	2.63
	TRIS MIN*	1.64	0.91	1.15	2.30	1.16
Celtic Sea	CALL MAC	1.71	0.24	1.07	2.42	1.35
	CONG CON*	2.34	0.95	0.80	6.34	5.54
	EUTR GUR*	0.75	0.74	0.18	1.40	1.22
	LOPH PIS*	0.86	0.57	0.27	1.67	1.39
	MICR VAR*	1.14	0.61	0.59	2.21	1.71
	RAJA BAI*	1.23	0.56	0.40	2.25	1.85
	SCOM SCO > 22	1.69	0.46	0.77	2.99	2.22
	ZEUS FAB	1.85	0.65	0.76	3.67	2.90

Note: The asterisk (*) corresponds to species for which a small proportion of bootstrap replicates b led to undefined $\hat{x}_b^*$. These replicates were excluded when computing bootstrap means and variances but were kept in CI computations because that proportion was very small (<1%).

Table 12. Species for which no reliable estimate could be obtained from the intercalibration data.

North Sea	Celtic Sea
BUGL LUT	CLUP HAR
CALL LYR	GAID VUL
ENCH CIM	HELI DAC
GLYP CYN	LIMA LIM
GOBI NIG	LOLI FOR
HELI DAC	LOPH BUD
LUMP LAM	MOLV MOL
MULL SUR	PHYC BLE
MUST AST	RAJA CLA
NEPH NOR	SQUA ACA
PLAT FLE	
SALM SAL	

The maximum quasi-likelihood estimator of the conversion coefficient is simple and valid under quite a wide range of conditions. This estimator would be expressed in the same way in a likelihood model based on the assumption of a Poisson process for catch. It would also correspond to a ratio estimator based on sampling theory (Cochran 1977). However, these estimators differ in their variances. In addition, in contrast to a likelihood approach that is conditioned on the realization of the underlying abundance at the time of the experiment, a quasi-likelihood approach is not conditional on abundance and is even valid under a wide range of distributions for this random variable. This allows one to make quite general assumptions about the underlying abundance process and corresponding spatial structure, i.e., spatial correlation and mean–variance relationship. These assumptions were not completely utilized when planning the survey and analyzing the intercalibration data because bootstrap estimates were used instead of asymptotic variances. However, the approach developed allows for estimating asymptotic variances as well as abundance parameters, the spatial correlation coefficient, and the parameter of mean–variance relationships. Because this paper focuses on the estimation of conversion coefficients, corresponding results were not reported here.

Unlike linear or log-linear models based on Gaussian assumptions, the statistical model used here captures the possibility of null catch through the sampling distribution of catch, which enables one to retain most of the valid data with the exception of zero catch for RV1. Although low and zero catch bring less information about conversion coefficients, this is interesting because the effective sample size is not decreased by excluding every pair that contains a zero catch. No arbitrary addition of a small value is needed to handle zero catch. To some extent, the statistical model used is more general and likely to be closer to reality in that it describes the randomness of both sampling and underlying abundance process. Within this model, skewed distributions do not pose any problem for estimation.

The bootstrap procedure used brings some advantages in that (*i*) the quality of the estimation is not only measured through the variance, but also through the bias; (*ii*) sample size is small and the asymptotic variance is theoretically

© 1998 NRC Canada

valid only for large sample sizes; and (*iii*) the sampling variability inherent to fisheries surveys is better accounted for from bootstrap estimates than by using the asymptotic variance. Although the maximum quasi-likelihood estimator of conversion coefficients (eq. 10) does not seem to account for paired hauls, this is explicitly achieved through bootstrap estimates because the bootstrap procedure resamples pairs of hauls, not catches of each vessel. Note that the asymptotic covariance matrix would also account for paired hauls. Two estimators of the asymptotic variance of $\hat{x}$ were indeed compared to the bootstrap variance. Unreported results showed that in this case, the former leads to numerically unstable results, reinforcing the idea that the bootstrap variance is more appropriate in this work in relation to a small sampling size. In contrast with the literature reviewed, the estimation method presented here is defined before the experiment takes place and is explicitely used in computer simulations to plan the survey. Therefore, sampling design and statistical model are fully consistent, and data analysis does not require any ad hoc procedure, e.g., data transformation to handle null catch.

No comparison with other designs, such as randomized plans, was carried out in this study because only an experiment was possible. Nevertheless, it seems that conducting a survey from paired hauls in small areas is preferable because the effects on estimation of the variability due to spatial heterogeneity are minimized. The experiment may then be carried out with a lesser number of hauls than in randomized plans. The simulations based on previous surveys allowed the careful selection of the most appropriate areas to conduct the intercalibration experiment. However, such a sampling design raises the question of the applicability of the obtained estimates to the rest of the region surveyed.

In light of this experiment and the existing literature, it seems that such experiments are at the same time necessary but not completely convincing because they are difficult to plan and to conduct. Carrying out a survey with two vessels that should fish in a synchronized way can pose considerable logistical difficulties. In the case of a new vessel, survey design should also account for the high probability of technical problems that may eventually lower the number of valid data. In addition, many intercalibration experiments report substantial tow-by-tow variation, even at small distances. To maximize the probability of conclusive results, particular attention should be payed to survey planning and to controlling as many sources of variability as possible during the experiment. Preliminary work based, for example, on computer simulations and prior information about ressources should definitely help in planning this type of experiment. Selecting areas of high abundance is indispensable in minimizing the risk of null catch, which brings no information and actually decreases the effective sample size. Lastly, gear monitoring is an indispensable tool in controlling some sources of catch variability.

Acknowledgements

The author wishes to thank Ana Parma, Stephen Smith, Paul Fanning, and an anonymous referee for many helpful suggestions on earlier versions of this paper.

References

Anonymous. 1992. Report of the workshop on the analysis of trawl survey data. ICES CM 1992/D:6.

Azarovitz, T.R. 1981. A brief historical review of the Woodshole Laboratory trawl survey time series. *In* Bottom trawl surveys. *Edited by* W.G. Doubleday and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. 58. pp. 62–67.

Bickel, P.J., and Doksum, K.A. 1977. Mathematical statistics. Prentice Hall, N.J.

Byrne, C.J., and Fogarty, M.J. 1985. Comparison of the fishing power of two fisheries research vessels. Northwest Atl. Fish. Organ. (NAFO) SCR Doc. 85/90.

Byrne, C.J., and Forrester, J.R.S. 1987. Effect of a gear change on a standardized bottom trawl survey time series. *In* Proceedings the Ocean — an international workplace, Halifax, Nova Scotia, Canada, Sept. 28 – Oct. 1, 1987. Vol. 3. *Sponsored by* Marine Technology Society, Institute of Electrical and Electronics Engineers, New York. pp. 611–621.

Byrne, C.J., and Forrester, J.R.S. 1991. Relative fishing power of NOAA R/V's *Albatross IV* and *Delaware II*. NEFC SAW/12/P1. Northeast Fisheries Center, Woods Hole, Mass.

Byrne, C.J., Azarovitz, T.R., and Sissenwine, M.P. 1981. Factors affecting variability of research vessel trawl surveys. *In* Bottom trawl surveys. *Edited by* W.G. Doubleday and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. 58. pp. 258–273.

Carrothers, P.J.G. 1981. Catch variability due to variations in groundfish otter trawl behaviour and possibilities to reduce it through instrumented fishing gear studies and improved fishing procedures. *In* Bottom trawl surveys. *Edited by* W.G. Doubleday and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. 58. pp. 247–257.

Cochran, W.G. 1977. Sampling techniques. 3rd ed. Wiley & Sons, New York.

Doubleday, W.G., and Rivard, D. 1981. Bottom trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci. 58.

Downing, J.A. 1986. Spatial heterogeneity: evolved behaviour or mathematical artefact? Nature (London), **323**: 255–257.

Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. Soc. Ind. Appl. Math. CBMS – Natl. Sci. Found. Monogr. **38**.

Ehrich, S. 1991. Comparative fishing experiments by research trawlers for cod and haddock in the North Sea. J. Cons. Int. Explor. Mer, **47**: 275–283.

Ehrich, S., Dahm, E., Dornheim, H., Lange, K., Mergardt, N., and Stein, M. 1994. Comparative fishing with FRVs "Walter Herwig" and "Walter Herwig III." ICES CM 1994/B:15.

Fanning, L.P. 1984. Preliminary analysis of Alfred Needler – Lady Hammond comparative fishing experiments (Silver Hake 1983). Northwest Atl. Fish. Organ. (NAFO) SCR Doc. N871.

Fanning, L.P. 1985. Intercalibration of research survey results obtained by different vessels. CAFSAC Res. Doc. 85/3.

Foster, J.J., Campbell, C.M., and Sabin, G.C.W. 1981. The fish catching process relevant to trawls. *In* Bottom trawl surveys. *Edited by* W.G. Doubleday and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. 58. pp. 229–246.

Gauthiez, F. 1994. Characterizing small-scale patterns in fish populations via Taylor's power law: an extended quasi-likelihood model. *In* Actes des Journées Internationales "Ecologie et méthodes statistiques." *Edited by* V. Bretagnolle and F. Béninel. CNRS, Niort, France. pp. 97–99.

Gavaris, S., and Brodie, W.B. 1984. Results of comparative fishing between the A.T. Cameron and the Wilfred Templeman during July–August 1983. CAFSAC Res. Doc. 84/41.

© 1998 NRC Canada

Godø, O.R. 1990. Factors affecting accuracy and precision in abundance estimates of gadoids from scientific surveys. Ph.D. thesis, University of Bergen, Bergen, Norway.

Godø, O.R., and Engås, A. 1989. Swept area variation with depth and its influence on abundance indices from trawl surveys. J. Northwest Atl. Fish. Sci. **9**: 133–140.

Koeller, P. 1991. Approaches to improving groundfish survey abundance estimates by controlling the variability of survey gear geometry and performance. J. Northwest Atl. Fish. Sci. **11**: 51–58.

Koeller, P., and Smith, S.J. 1983. Preliminary analysis of A.T. Cameron – Lady Hammond comparative fishing experiments 1979–1981. CAFSAC Res. Doc. 83/59.

Mitson, R.B. 1992. Underwater noise radiated by research vessels. ICES Mar. Sci. Symp. **196**: 147–154.

Perry, J.N. 1981. Taylor's power law for dependence of variance on mean in animal populations. Appl. Stat. **30**: 254–263.

Robson, D.S. 1966. Estimation of the relative fishing power of individual ships. Int. Comm. Northwest Atl. Fish. Res. Bull. **3**: 5–14.

Sissenwine, M.P., and Bowman, E.W. 1978. An analysis of some factors affecting the catchability of fish by bottom trawls. Int. Comm. Northwest Atl. Fish. Res. Bull. **13**: 81–87.

Smith, S.J. 1997. Bootstrap confidence limits for groundfish trawl survey estimates of mean abundance. Can. J. Fish. Aquat. Sci. **54**: 616–630.

Taylor, R. 1961. Aggregation, variance and the mean. Nature (London), **189**: 732–735.

Warren, W.G. 1996. Report on the comparative fishing trial between the Gadus Atlantica and Teleost. Northwest Atl. Fish.Organ. (NAFO) SCR Doc. 96/28.

Wedderburn, R.W.M. 1974. Quasi-likelihood functions, generalized linear models, and the Gauss–Newton method. Biometrika, **61**: 439–447.

Appendix. Description of the bootstrap procedure

Given a reference sample of paired hauls, a point estimate $\hat{x}_{\text{ref}}$ is estimated from eq. 10. The reference sample is also used to estimate an empirical probability distribution function (PDF) of the pairs of data. The resampling procedure explicitly captures the paired nature of hauls because, in a given area, pairs of catch are resampled with replacement and with equal probabilities. B replicates of the data are generated using this PDF. For each replicate, an estimate $\hat{x}^*_b$ is obtained and bootstrap estimates are computed as follows:

$$\hat{x}^* = \frac{1}{B}\sum_b \hat{x}^*_b$$

$$\text{(A.1)}\quad \hat{B}(\hat{x}^*) = \frac{1}{B}\sum_b (\hat{x}^*_b - \hat{x}_{\text{ref}})$$

$$\hat{V}^*(\hat{x}^*) = \frac{1}{B}\sum_b (\hat{x}^*_b - \hat{x}^*)^2$$

$\hat{V}^*(\hat{x}^*)$ may be a better indicator of the sensitivity of the estimator of x to sampling variability than estimates of the asymptotic variance of $\hat{x}$. It may also be a better variance estimator for small sample sizes.

The quality of the estimation is tied to both the accuracy and the precision of the estimate $\hat{x}^*$. The mean square error of the estimator is thus appropriate to evaluate the quality of the estimation:

$$\text{MSE}^*(\hat{x}^*) = \hat{V}^*(\hat{x}^*) + \hat{B}^*(\hat{x}^*)^2$$

In addition, because the conversion coefficient will likely differ among species, the relative root mean square error (RMSE) should be used.

$$\text{(A.2)}\quad \text{RMSE}^*(\hat{x}^*) = \frac{1}{\hat{x}_{\text{ref}}}\sqrt{\text{MSE}^*(\hat{x}^*)}$$

$\text{RMSE}^*(\hat{x}^*)$ is analogous to a coefficient of variation for the mean square error. Defining a relative value will facilitate comparisons of results among species.

Confidence intervals may be computed for the conversion coefficients. A method for estimating nonparametric bootstrap intervals is described in Efron (1982). An application to fisheries survey data may be found in Smith (1997). In the present application, no correction for bias was used because the value of the criterion suggested by Efron (1982, p. 82) showed that this was not necessary. Because the estimation of confidence intervals requires an estimation of the percentiles of the distribution of the estimates $\hat{x}^*_b$, a larger number of replicates is needed than to estimate RMSEs.

© 1998 NRC Canada

Evaluation of quota management policies for developing fisheries

Carl Walters

Abstract: Losses can be measured as deviations from a desired reference trajectory of quotas that would be taken if there were no uncertainty and are highly dependent on assessments prior to and during development. Simulations of assessment and quota setting under various quota setting rules indicate that variability in relative abundance indices can cause substantial losses, especially considering cumulative effect of early quota errors on later departures of biomass from that needed to produce the desired quotas, even if optimum fishing mortality rate is known in advance. Conservative assessments (low biomass estimates for which there is only a small probability that biomass is actually lower) are favored during development when loss is measured as the relative departure from the best quota for each year. But if loss is measured as absolute departure from the best quota, it is generally better to base the quota on the biomass estimate for which there is nearly a 50% chance that the stock is smaller. Deliberate overfishing (probing) is not favored under either loss measure. Losses can be reduced with minimum biomass surveys and closed areas that directly cushion fishing mortality rates from being more than 50% too low or high.

Résumé : Les pertes peuvent être mesurées comme écarts par rapport à une courbe de référence souhaitée des quotas qui seraient pris en l'absence d'incertitude, et elles sont fortement dépendantes des évaluations faites avant et après le développement de la pêche. Les simulations de l'évaluation et de l'établissement des quotas selon diverses règles indiquent que la variabilité des indices de l'abondance relative peuvent causer des pertes substantielles, surtout lorsqu'on tient compte de l'effet cumulatif des erreurs initiales dans les quotas sur les écarts ultérieurs de la biomasse par rapport à celle qui serait nécessaire pour produire les quotas souhaités, même si on connaît à l'avance le taux optimal de mortalité par pêche. Il est conseillé d'avoir recours à des évaluations prudentes (estimations basses de la biomasse pour lesquelles n'existe qu'une faible probabilité que la biomasse soit effectivement plus basse) pendant la phase de développement lorsque la perte est mesurée comme écart relatif par rapport au meilleur quota pour chaque année. Toutefois, si on mesure plutôt l'écart absolu par rapport au meilleur quota, il vaut généralement mieux baser le quota sur l'estimation de la biomasse pour laquelle il y a près de 50% de chances que le stock soit plus petit. Quelle que soit la méthode de mesure des pertes, il n'est pas recommandé d'avoir recours délibérément à la surpêche (à titre exploratoire). On peut réduire les pertes en effectuant des relevés de la biomasse minimale et en fermant des zones qui permettent directement d'éviter que les taux de mortalité par pêche soient de 50% trop haut ou trop bas.

[Traduit par la Rédaction]

Introduction

There is surprising demand today for development of new fisheries due to desperation of fishers displaced from collapsed fisheries and to emergence of New World markets for edible products from aquatic ecosystems. From a stock assessment perspective, new fisheries can no longer be studied at leisure by counting on efforts and catch to develop slowly enough to provide clear signals of stock decline well in advance of serious overfishing. Usually, surplus fishing capacity and technology are more than capable of quickly doing very severe damage to almost any natural population.

As capacity for destructive development has grown, so has public demand for sustainable management and for new cost and risk sharing arrangements (Troadec 1989; Pearse and Walters 1992; Walters and Pearse 1996; Starr et al. 1998). Fishers are often expected to share the costs of "proving" potential through investment in exploratory fishing, regular surveys, basic biological research, and better record keeping. Fishers are demanding better value for their money: there is less tolerance for basic research, poorly designed surveys, and inept assessments. Also, there is growing demand by both fishers and fishery managers for output controls (quota management), with obvious economic and administrative advantages but dangerous in a world where fishing technologies are capable of taking quotas that are grossly too high.

This paper uses simulation of data gathering and assessment (Smith 1993) to define when improved information gathering is likely to result in substantially improved management for developing fisheries, defined here as situations where (*i*) fishing mortality has historically been low or negligible, (*ii*) a stock is near an unfished level most often involving considerable biomass accumulation that cannot be sustained under harvesting, and (*iii*) there is enough economic demand for growth in fishing mortality to eventually cause overfishing. Performance is measured by deviations of yield from a desirable reference trajectory that would be taken given no uncertainty about stock size; both positive and negative deviations from the desirable trajectory are

Received February 11, 1998. Accepted August 4, 1998.
J14446

C. Walters. Fisheries Centre, University of British Columbia, Vancouver, BC V6T1Z4, Canada. e-mail: walters@fisheries.com

© 1998 NRC Canada

treated as loss. I argue that such errors arise less from uncertainty about productivity (best fishing mortality rate) than from uncertainty about total stock size. Three approaches are suggested for reducing the impact of assessment errors on long-term performance: (*i*) progressive exposure to increasing fishing mortality, with only a small part of any stock exposed at first to risk of harvest, (*ii*) limits on fishing mortality independent of stock size assessments via spatial closures that reduce the proportion of fish exposed to harvest risk, and (*iii*) surveys by industry to provide minimum estimates of occupied area and density that can be used to set quota "floors" or "proven production potential" directly.

Modeling development as an adaptive process

Presumably, management for new fisheries aims to regulate harvests so the stock(s) will move to a most productive level for sustaining yield without passing through a costly period of collapse. Usually, we cannot tell how large a stock is without exploiting it, and we cannot be sure that a most productive level has been reached without obtaining observations from stock sizes below that level (Hilborn and Sibert 1988). In short, developing fisheries live and die by the quality of information used to learn about sustainability: new management strategies for developing fisheries should be based on understanding limits to learning and on regulatory tactics to prevent destruction before good information becomes available.

Can we resolve the dilemma posed by Hilborn and Sibert (1988) by breaking down the problem of assessing long-term quotas into simpler subproblems and by making judicious use of previous fishery development experience? A best long-term regime is defined by average catch quota C_1, average biomass B_1, and optimum fishing mortality rate F_{opt} so that $C_1 = F_{opt}B_1$. Thus the adaptive process of learning about sustainable catch has two subproblems: (*i*) F_{opt}, which depends on growth, natural mortality, and recruitment compensation parameters, and (*ii*) B_1, which depends on many factors ranging from simple habitat size to life history characteristics that define how good fish are at utilizing resources and dealing with risks in the habitat.

We can obtain bounds on F_{opt} from basic information on growth and natural mortality rates M. Empirical experience suggests that F_{opt} is generally less than or equal to M and, at least for pelagic species, is most likely to be on the order of $2/3M$ (Patterson 1992). Further, setting a target F somewhat lower than optimum (e.g., $2/3M$ when $F_{opt} = M$) is not costly in terms of lost harvest opportunity, since this lower F will result in a higher average biomass so the product FB is not substantially lower than $F_{opt}B$. In short, we can solve "half" of the problem of assessing an optimum long-term quota C_1 quickly by investing in acquisition of good growth and natural mortality information very early in (or as a precondition for) fishery development. That is, we can avoid part of the dilemma posed by Hilborn and Sibert (1988) by accepting modest losses in potential yield, without determining F_{opt} precisely by seeing what happens if it is exceeded. Considering progress in methods for sampling and aging aquatic organisms, there are few potential fisheries for which the investments needed to obtain this information would be too costly for fishers and public agencies.

Given good estimates of F_{opt} from previous fisheries experience and knowledge about aquatic organisms, the difficult problem is then to either estimate the stock size B_t over time or find a way to directly regulate F (e.g., through large marine protected areas). Quota management appears to preclude the second of these options, leaving estimation of B_t as the main adaptive learning problem. Unlike F_{opt}, population dynamics theory and experience tell us almost nothing about what B_1 values to expect (although that experience does provide likely values for the ratio of B_1 to unfished stock size B_0).

Seldom can we economically estimate biomass through direct enumeration. The B_t is a product of mean density per unit habitat area, $(B/A)_t$, and area occupied, A_t, i.e., $B_t = (B/A)_t A_t$. We can rarely afford to obtain large enough samples of $(B/A)_t$ to estimate mean density accurately, and in most developments, A_t is also highly uncertain and is "discovered" by fishers in search of better fishing opportunities. Experience and trophic theory may provide bounds for density $(B/A)_t$ but not for A_t. Further, A_t can change rapidly due to environmental influences, and factors like shoaling behavior can cause A_t to decrease as B_t declines. Fishery-independent biomass surveys help guard against errors in assessment of $(B/A)_t$ due to nonrandom targeting of high-density sites by fishers, but it is usually not economical to spread survey sampling over large enough areas to insure against errors in assessment of A_t; further, if surveys represent only areas of major fish concentration, survey abundance indices can show the same "hyperstability" (Hilborn and Walters 1992) as commercial catch rate during stock declines, if occupied range area contracts into the surveyed area.

Because of technical difficulties and costs of assessing $(B/A)_t$ and A_t, B_t must usually be estimated with some generalized "removal method": we compare measured total removals (catches) with survey or catch rate indices of relative abundance so as to reconstruct how large the stock had to have been to produce both the removals and the observed trend in relative abundance. Such comparisons involve fitting population models to the relative abundance data, where we "drive" the models with observed removals and also correct the abundance predictions for effects of production processes (growth, recruitment, natural mortality). Models range from simple biomass dynamics equations based on surplus production or delay-difference relationships to complex age-structured models that simulate losses either forward over time ("synthesis" models: Fournier and Archibald 1982; Deriso et al. 1985; Megrey 1989; Methot 1990; Schnute and Richards 1995) or backward (virtual population models, e.g., ADAPT: Gavaris 1988; Walters and Punt 1994). There are pitfalls with all of these removal models, particularly in relation to violation of assumptions about the abundance index being proportional to B_t. And generally, the more complex age-structured models do not perform all that much better than the simple ones (Hilborn 1979; Ludwig and Walters 1985; NRC 1997; Punt 1997); the massive increase in apparent information associated with age composition data is useful mainly for estimating recruitment variation and age–size selectivity.

© 1998 NRC Canada

For removal models to perform well, catches must cause large changes in relative abundance. In adaptive management terms, this means that there is a strong "dual effect of control" (Walters 1986): harvests produce both direct value and information value in the form of impacts on relative abundance. There is a conflict between the dual effects: harvesting harder promotes faster learning, but also increases risk of overfishing. Little progress has been made toward solving the formal dynamic optimization problem of how to best balance the dual effects; suggestions about how to approach this problem have ranged from dynamic programming methods (Walters 1986) to management "metagaming" (Walters 1994).

Some assessments of overharvesting risk during development have ignored the dual effect of harvesting on information. For example, one practice has been to simulate alternative future quota sequences while assigning probabilities to various estimates of unfished biomass and productivity and then report the resulting probabilities of reducing stock size below some arbitrary threshold level. A fisher or manager could ask "but if unfished biomass is in fact low, will relative abundance not decline more quickly and give opportunity to correct the quotas much sooner than in your simulations?" This is a valid question; there is no good excuse to ignore future data gathering and response to new information. We can predict, or specify as investment options, the data gathering and analysis methods that will be used, and we have enough experience with variability in survey and catch rate data to simulate likely patterns of stochastic variation. Thus, we can simulate future observations of relative abundance (and age composition, etc.) and assessment calculations based on these. Such "closed-loop" simulations (Smith 1993) of future management performance have other benefits; in particular, they allow us to compare various decision rules for responding to uncertainty. That is, using closed-loop simulations, we can answer questions like "what if future decisions are based on setting the quota each year to $F_{opt}B_{0.1}(t)$ where $B_{0.1}(t)$ is the 10% point on the cumulative probability distribution for B_t (value of B for which there is a 90% chance that B_t is actually larger) and how will expected yields from this option compare with harvesting $F_{opt}B_{0.5}(t)$?"

Procedures for assessing performance of development strategies

One way to compare closed-loop policies is to simulate development performance for a range of alternative hypotheses about unfished stock size and then use a weighted average of performance over this range as an overall measure. The function used to measure performance under each alternative hypothesis is a "loss function" and the weighted average of this function over hypotheses is the "risk" (Mood and Graybill 1963). Statistical decision theory encourages us to use Bayes prior probabilities $P_0(B_0)$ for unfished biomasses B_0 as weights for calculating risk; leaving out such weights (just averaging performance over a wide range of B_0 values) is equivalent to assuming equal prior probabilities for all values of B_0 admitted in analysis. This raises an important basic issue and warning to the reader: we cannot measure or quantify risk for any particular development opportunity without at least placing bounds on possible B_0 outcomes, and the choice of bounds is necessarily subjective. Hence, any procedure for assessing risk is vulnerable to abuse: analysts can paint an unduly conservative or rosy picture of future risk by appropriate choice of B_0 bounds.

Performance simulations need six basic components: (*i*) bounds on uncertainty in the form of parameters that are taken to be known or given (not treated as part of the simulated learning process) and prior range for B_0, (*ii*) a population response submodel for predicting how any catch sequence would influence B_t, given any B_0, (*iii*) an observation submodel for generating simulated future observations given any B_t, (*iv*) a procedure to simulate how future observations will be used to update a probability distribution $P_t(B_t)$ for biomass (and perhaps other uncertain quantities), (*v*) a procedure for translating the probability distribution $P_t(B_t)$ into specific quota decision choices C_t (i.e., a procedure for applying decision rules based on P_t), and (*vi*) a procedure for calculating performance from each simulation trial over $t = 1,..., T$ years. Results presented here are based on simulation component assumptions described in the following subsections.

The procedures described below are not meant to represent the best modeling or Bayesian data analysis. Various procedural simplifications are used to make it computationally practical to compare very large numbers of simulation trials. I tried to use simplifications that avoid overly optimistic estimates of future uncertainty, although most modern procedures would deal explicitly with some uncertainties that I ignore or lump with others. Unfortunately, even the relatively optimistic assumptions used below are not enough to rescue some commonly held beliefs about the value of assessment information during fishery development; I show that even where these optimistic assumptions are valid, assessment information cannot usually be gathered quickly or accurately enough to prevent substantial risk during development.

Baseline information assumed to be available at the start of development

There are at least two ways to set a good simulation estimate of F_{opt}: (*i*) obtain an estimate of natural mortality rate M and take $F_{opt} = 0.6M$ (Patterson 1992; Mertz and Myers 1998) and (*ii*) obtain an estimate of M and of the Ford–Brody growth parameters and (intercept and slope of the body weight Walford plot) and use these along with recruitment parameters in an equilibrium delay-difference model to calculate F_{opt} (Walters and Parma 1996). Since information on recruitment compensation will generally not be available at the start of development, the second of these approaches is most likely to be "tuned" (by varying the ratio of maximum to unfished recruitment per biomass) so as to give F_{opt} on the order of 0.6–1.0M. I assume below that F_{opt} has been correctly estimated from early biological sampling and analysis efforts. Thus the pathological estimates of expected losses presented below are due only to biomass estimation problems; including effects of errors in estimation of F_{opt} would result in even higher loss estimates.

I also assume that there has been enough exploratory fishing or surveys to provide swept area or local depletion estimates of density and bounds for the area occupied. Products

© 1998 NRC Canada

of these estimates are assumed to provide bounds B_{min} and B_{max} for unfished biomass B_0. The prior distribution $P_0(B_0)$ is then assumed to be uniform over B_{min} to B_{max}. The evaluation examples presented below are generally based on very wide limits, e.g., from $1 \times C_0$ to $300 \times C_0$, where C_0 is average catch over a few years prior to the first risk analysis.

Alternative loss functions for comparing development policies

Many measures can be used to compare performance of alternative information gathering and regulatory policies for developing fisheries, ranging from simple output measures like total catch over an arbitrary development period, to discounted economic value, to risk of having the stock fall below some arbitrary threshold value relative to B_0. Comparison of simple biological or economic output measures is complicated by failure of these measures to recognize some development objectives that are difficult to quantify. For example, total catch is generally maximized by a policy that takes high catches initially so as to drive the stock to an optimum level as quickly as possible and then much lower catches afterward; however, there are social and economic drawbacks to such a boom–bust trajectory. Likewise, it is hard to justify policies based on avoiding arbitrary biomass levels; we generally cannot decide objectively what a "dangerous" biomass level is, nor can we expect full consensus from fisheries stakeholders on an acceptable probability (or risk) of falling below any such level.

One way to represent complex temporal objectives is to measure performance as a loss relative to some arbitrary trajectory of catches that would be chosen by stakeholders if they had perfect knowledge of stock size and future production. That is, suppose we knew B_0 and F_{opt} exactly, along with future recruitment anomalies. Then, I expect that we could obtain consensus on an optimum quota development trajectory of the form

$$(1) \qquad C_{opt}(t) = D(t)F_{opt}B_t,\ t = 1,\ldots,\ T$$

where $D(t) \leq 1.0$ represents a "fractional development" or progressive development function set to increase over time so that catch approaches $F_{opt}B_t$ in the long term. Note that constraining D to be <1.0 means insisting that F never exceed F_{opt} and hence that expected biomass B_t never be driven below the optimum equilibrium resulting from B_1, i.e., eq. 1 with $D < 1$ implies a mandatory concern for long-term sustainability, whatever stakeholders might feel about how rapidly development should proceed.

For simulation tests, I assume that stakeholder consensus will result in a $D(t)$ that increases asymptotically toward 1.0 (F starts low and approaches F_{opt} over time), and for simulation tests, I assume that D can be approximated by a function of the form

$$(2) \qquad D(t) = (t/t_h)/[1 + (t/t_h)].$$

In this formulation, t_h is the number of years until the fishing mortality rate would be allowed to reach $1/2F_{opt}$; setting high values for t_h would result in "smooth" development without an initial overshoot of C_t to values above the long-term sustainable level C_1. Then, suppose that an information gathering/response policy results in the catch sequence $C_{real}(t)$, where the policy accounts for development objectives represented in $D(t)$ but differs from C_{opt} due to errors in assessment of B_t, use of deliberately cautious B_t estimates, and cumulative impacts of past C_{real} quota choices on B_t. We can measure the loss L due to using this policy in at least two simple ways:

Sum of absolute quota errors:

$$(3a) \qquad L_{abs} = \sum_{t=1}^{T} \left| C_{opt}(t) - C_{real}(t) \right|.$$

Sum of relative quota errors:

$$(3b) \qquad L_{rel} = \sum_{t=1}^{T} \left| C_{opt}(t) - C_{real}(t) \right| / C_{opt}(t).$$

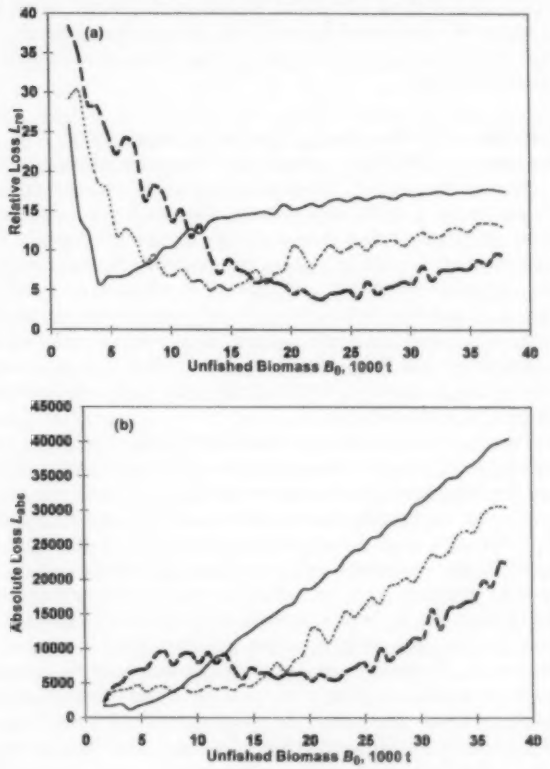
Both of these loss measures are based on two key presumptions: (*i*) future losses are as important as present ones, at least for T years (i.e., no discounting of future losses), and (*ii*) quota overages ($C_{real} > C_{opt}$) are as undesirable as missed opportunities ($C_{real} < C_{opt}$), whether or not the overages result in any long-term impairment of capability to achieve C_{opt} due to impact on B_t. Simulation trials indicate that inclusion of low discount rates (0.01–0.03 per year) does not substantially affect policy comparisons based on L, but differential weighting of overages and underages can have a profound effect (failing to penalize overages makes aggressive development policies look better unless T is large enough for long-term losses due to overfishing to become clearly evident).

Although eqs. 3*a* and 3*b* appear to weight over- and under-fishing equally, the absolute and relative loss measures result in profoundly different relationships between loss and initial population size B_0 and hence very different weighting of over- versus under-harvesting when risk or expected loss is calculated as a weighted sum of losses over the prior probability distribution for B_0. The basic difference (Fig. 1) is that the relative loss measure strongly penalizes quota overages early in development and (or) for low values of B_0 (cases when C_{opt} is in fact small) but "unweights" losses when C_{opt} is in fact large (if B_0 is in fact large, or later in development). In contrast, the absolute loss measure is small for low B_0 whether or not the quota policy wipes out this small biomass but is large for high B_0 when the quota policy does not fully capitalize on the harvest opportunity represented by this high B_0. In short, the relative measure penalizes overharvesting relative to whatever potential the stock turns out to have (whatever B_0 really is) whereas the absolute measure places much more weight on losses in total catch. Hence the relative measure tends to favor cautious policies (do not risk overharvesting in the event that B_0 is small) whereas the absolute measure tends to favor "certainty equivalent" (Walters 1986) policies (assume that B_0 is somewhere in the middle of its probable range).

There are reasons for preferring either absolute or relative loss as performance measures. An "ecologically" oriented stakeholder might argue for the relative measure on the grounds that development should aim to bring fishery resources to their best potential whatever that potential might happen to be, with relatively low risk of overfishing during the development. But a "socially" oriented stakeholder

© 1998 NRC Canada

Fig. 1. Simulated variation in 20-year (*a*) relative and (*b*) absolute losses measured as differences between quotas realized and reference or target quotas. Note that relative loss is higher for low unfished biomass (overfishing risk weighted heavily), while absolute loss is highest for high stock size (underfishing risk weighted heavily). Each point along a curve is mean of 10 simulation trials. Quotas were set each simulated year using the biomass estimate for which assessment indicated probability ξ that the stock size was actually smaller. Solid line, $\xi = 0.1$; dotted line, $\xi = 0.3$; heavy broken line, $\xi = 0.5$.



might equally well argue that total yield (and the economic development potential it represents) is what really matters to people and that the risk of overharvesting a resource that cannot support much development should not be considered important. This is a debate that proponents and regulators of development must somehow resolve. Absent better arguments to the contrary, agency regulators today are becoming more likely to adopt relative loss measures that reflect public concern about biological diversity and the protection of vulnerable species and stocks.

For simulation tests, I elected to use relatively short planning horizons T of 20–40 years for two reasons. First, if major deviations (losses) from a desired development pattern are going to occur because of inadequacies in information gathering and assessment methods, these deviations will be concentrated in the first few decades of development. Second, I tested longer horizons and found that these did not affect predicted loss patterns and relationships between loss and policy variables intended to reduce loss.

Representation of uncertainty as development proceeds

As noted above, we generally represent uncertainty about current biomass B_t by measures of how well alternative hypotheses about the biomass trajectory (removal pattern) agree with observed indices Y_t of relative abundance. Here, I assume that relative abundance will be measured over time (using standardized catch-per-unit-effort (CPUE) or surveys) so as to follow the multiplicative observation error model

$$(4) \qquad Y_t = q B_t^{\beta} \exp(v_t \sigma_v)$$

where v_t is normally distributed with unit standard deviation and the nuisance parameters q, β, and σ_v are unknown except for the following prior probability statements: (*i*) all values of $\ln(q)$ are equally likely, (*ii*) the prior probability for σ_v is proportional to $1/\sigma_v$ (Jeffreys prior), and (*iii*) all values of β between β_{min} and β_{max} are equally likely (the worst case is hyperstability: $\beta_{min} = 0$, $\beta_{max} << 1$). Under these assumptions, the marginal likelihood (integrated over nuisance parameters) of Y ($Y = \{Y_1, ..., Y_T\}$) for any value B_0 is proportional to

$$(5) \qquad L(Y|B_0) = \int_{\beta=\beta_{min}}^{\beta=\beta_{max}} SS(\beta, B_0)^{-(T-1)/2}$$

where $SS(\beta, B_0)$ is the conditional (on β, B_0) sum of squared deviations

$$(6) \qquad SS(\beta, B_0) = \sum_{t=1}^{t=T} [z(t) - \bar{z}]^2$$

and

$$(7) \qquad z_t = \ln(Y_t) - \beta \ln[B_{B(0)}(t)].$$

Here, the notation $B_{B(0)}(t)$ refers to the most likely value of B_t given B_0, which we would most simply calculate by a deterministic simulation starting at B_0 and proceeding forward in time with removal at each t of observed catch. Equations 5–7 are simple extensions of derivations in Walters and Ludwig (1994). For simulation studies of estimation performance, note that Y_t is generated from eq. 4 with an arbitrary true q and biomass sequence $B_{trueB(0)}(t)$ and note that SS can be calculated efficiently at each simulated t by updating the sufficient statistics

$$(8) \qquad \begin{aligned} S_1(\beta, B_0) &= \sum z_t^2 \\ S_2(\beta, B_0) &= \sum z_t \end{aligned}$$

and using the familiar statistical relationship $SS = S_1 - S_2^2/T$. For the results presented below, I stored S_1 and S_2 values for a 10 × 50 grid of β, B_0 combinations ($\beta = (\beta_{min} + \beta_{max} - \beta_{min})i/9$, $i = 0, ..., 9$; $B_0 = (B_{min} + B_{max} - B_{min})j/49$, $j = 0, ..., 49$) as each simulation proceeded and took the integral in eq. 5 to be just the sum of $SS^{-(T-1)/2}$ values over the β grid elements for each B_0. Further, I generally used $\beta_{min} = 0$, $\beta_{max} = 1$; this assumption ignores the possibility of hyperdepletion in the relative abundance index due to "mining" high-density fish aggregations that do not reform rapidly due to shoaling behavior, but does admit a risk of hyperstability in the relative abundance data. It is not assumed that the simulated manager knows the arbitrary q used to generate Y_t; in-

© 1998 NRC Canada

formation about q at each time t is available through the mean of z_t in eq. 7, which is the maximum likelihood estimate of $\ln(q)$, but this information is not used directly in setting simulated quotas.

A posterior probability distribution for B_0 is defined from the likelihood eq. 5 and prior probabilities $P_0(B_0)$ by

$$(9) \quad P_t(B_0|Y) = L(Y|B_0)P_0(B_0) \Big/ \int_{B_0=B_{min}}^{B_0=B_{max}} L(Y|B_0)P_0(B_0)\mathrm{d}B_0$$

Assuming that the P_0 and L values have been stored or calculated for a reasonably fine (e.g., 50-point) grid of discrete B_0 values, the posterior P_t for each discrete B_0 is found simply by summing the LP_0 values for all these B_0 and then dividing the LP_0 for each B_0 by that sum. For the assumptions outlined above, generally, P_t as a function of B_0 has a log-normal shape but is truncated at the biomass limits B_{min} and B_{max}. Further, admitting a wide range of possible values for β results in higher P_t for lower values of B_0, i.e., the admission that stock size may have decreased due to historical catches C_t much more than would be indicated by assuming Y_t proportional to biomass.

Accumulating the P_t values from eq. 9 as they are calculated results immediately in estimates of another important probability distribution, namely $P(B_t \geq X)$, which is the total of all P_t for which $B_{B(0)}(t) \geq X_t$, i.e., the odds that B_0 was high enough that B_t exceeds X given the history of catches up to time t. Then from this cumulative distribution, it is easy to pick out critical biomass estimates $B_\xi(t)$ for which the probability that $B_t \geq B_\xi(t)$ is ξ. For example, $B_{0.1}(t)$ is a "risk-averse" or conservative biomass estimate (only 0.1 probability that $B_t < B_{0.1}(t)$), while $B_{0.5}(t)$ is a "median" biomass estimate for which there is a 50:50 chance that biomass is actually lower.

An efficient computational technique when many simulations need be conducted for risk analysis is to simultaneously calculate the conditional biomass trajectories $B_{B(0)}(t)$ for all B_0 grid points as each simulation proceeds (Walters 1994). The delay-difference model for these trajectories is

$$(10) \quad B_{B(0)}(t) = S_{B(0)}(t-1)[\alpha N_{B(0)}(t-1) + \rho B_{B(0)}(t-1)] + w_k R_{B(0)}(t)$$

$$(11) \quad N_{B(0)}(t) = S_{B(0)}(t-1)N_{B(0)}(t-1) + w_k R_{B(0)}(t)$$

where the conditional survival rate $S_{B(0)}(t-1)$ is given by

$$(12) \quad S_{B(0)}(t-1) = \max\{0,[1 - C_{t-1}/B_{B(0)}(t-1)]e^{-M}\}$$

and recruitment $R_{B(0)}(t)$ is predicted from a stock–recruitment relationship of the form

$$(13) \quad R_{B(0)}(t) = aB_{B(0)}(t-k)/[1 + bB_{B(0)}(t-k)]^c \exp(w_t).$$

Here, a, b, and c are recruitment parameters, k is age at recruitment/maturity, and w_t is an arbitrary recruitment "anomaly" sequence with mean 0 over time. For simulation years 1 to k, R is initialized at $R_{B(0)}(0) = N_{B(0)}(0)(1 - e^{-M})$ (i.e., recruitment to the unfished stock just balances natural mortality on average) where $N_{B(0)}(0)$ is calculated from B_0 and predicted mean body weight for the unfished state as $N_{B(0)}(0) = B_{B(0)}(0)/\{[e^{-M}\alpha + w_k(1 - e^{-M})]/[1 - \rho e^{-M}]\}$ (Hilborn and Walters 1992). For results below, c is set to 1.0 (Beverton–Holt recruitment function), a is set to $5 \times R_{B(0)}(0)/B_0$ (recruits/spawner can increase to 5 times the unfished ratio if B is low), and b is calculated from a and $R_{B(0)}(0)$ so as to predict $R_{B(0)}(0)$ when $B_{B(0)}(t) = B_0$. The recruitment anomaly sequence w_t is either set to 0.0, in which case the "observation errors" v_t in eq. 4 are "contaminated" by correlated effects of historical recruitment anomalies (B_t varies from the mean prediction of the deterministic model; effect seen in deviations along with index measurement errors), or set to a sequence w_t assumed known from independent analysis of recruitment variation using age composition or recruitment index sampling.

Decision rules for relating quotas to uncertainty: biomass probabilities, progressive exposure plans

Any quota choice C_t can be thought of as arising from or rationalizing a particular probabilistic stock size estimate $B_\xi(t)$, in the sense that we can always express that choice C_t as a product, $C_t = D(t)F_{opt}B_\xi(t)$, and provided the target fishing mortality rate $D(t)F_{opt}$ is defined in advance as a desirable exploitation rate for year t. Recall from above that $B_\xi(t)$ is the stock size for which assessment procedures indicate a probability ξ that B_t is actually smaller. That is, ξ is the probability that if quota C_t is taken, the ratio C_t/B_t will exceed $D(t)F_{opt}$ at least for year t.

Thus, alternative decision rules for setting C_t can be expressed as choices of the progressive exposure function $D(t)$ and the acceptable overharvest "risk" ξ, along with rules for processing the historical data so as to arrive at the estimator $B_\xi(t)$ for each year. An important point is that $B_\xi(t)$ is not a point biomass estimate based only on information (e.g., a survey) gathered prior to fishing in year t; the probability distribution for B_t from which $B_\xi(t)$ is calculated should reflect (summarize) all information gathered up to time t concerning B_t. Generally, such probability distributions cannot be represented completely by one or a few "information state" statistics, precluding the possibility of using optimization methods like dynamic programming to calculate an optimum feedback relationship between the quota choice C_t and current information state. To define decision rules for management practice, we are forced to guess at the likely form of the feedback relationship, and an obvious guess is that this relationship would involve acting as though ξ were constant, i.e., operate with the same overfishing risk each year.

Treating the risk measure ξ as a decision rule constant, with $\xi << 0.5$, does not mean that quotas will always be much lower than if the best biomass point estimate (roughly, $B_{0.5}(t)$) were used to calculate the quota. If good information is gathered during the development (accurate relative abundance data, informative biomass depletion pattern prior to time t), the probability distribution for B_t will become progressively more peaked around $B_{0.5}(t)$, so that $B_\xi(t)$ will approach the most likely estimate over time. Hence the simple decision rule $C_t = D(t)F_{opt}B_\xi(t)$ will "automatically" adjust for improving stock information over time, with $B_\xi(t)$ moving closer and closer to $B_{0.5}(t)$. This means that we probably do not need to evaluate policy rules that involve varying ξ over time (e.g., start with a low, risk-averse ξ and then move

© 1998 NRC Canada

toward $\xi = 0.5$ as better information becomes available), except to the extent that we should be concerned whether low values of ξ and (or) $D(t)$ may prevent the distribution of B_t from improving over time (lack of informative impact of quotas on relative abundance).

Using a constant ξ decision rule, $\xi < 0.5$, creates an economic incentive for gathering information that will narrow the B_t distribution, moving $B_\xi(t)$ closer to $B_{0.5}(t)$. There is, of course, always a risk that better information will reveal B_t to be near the lower end of the B_t distribution, but on average, at least some investment should be a good gamble. The possibility that ξ should be set very low, so that $B_\xi(t)$ represents a "proven production potential", has been discussed by Pearse and Walters (1992) and Walters and Pearse (1996). The effect of such incentives on information gathering to reduce σ_v or provide direct biomass estimates B_t is not represented in the analysis below. However, I do consider the impact on expected loss due to having industry invest in independent information gathering to provide a lower bound or "proven" estimate $B_{min}(t)$ represented as a proportion $R_{min}B_t$. Surveys to establish quota floors are different from surveys to provide trend indices Y_t for routine stock assessment; surveys for trend information must be done in a consistent way every year, while surveys to estimate a minimum proven production potential might vary greatly in area surveyed and survey methods depending on how much investment in "proving up" biomass is economically worthwhile. Such surveys affect likelihood calculations by setting the minimum B_0 and B_t for which nonzero likelihood should be assigned, but should not otherwise affect likelihoods assigned to higher B_t values based on trend data.

Likewise, I consider the impact of using regulatory measures like marine protected areas to provide an upper bound on the realized exploitation rate, $R_{max}F_{opt}$, where $R_{max} > 1$. The idea here is that measures like large spatial closures can limit the fraction of the stock exposed to significant risk of capture, except perhaps for highly migratory species.

While fixed exploitation rate policies of the form $C_t = FB_t$ may assure near-optimum long-term harvest performance in the face of variation in recruitment due to environmental changes (Walters and Parma 1996; Engen et al. 1997), it is not clear that such policies are best for dealing with the contingency $B_t << B_t$, i.e., accidental reduction of stock size to far below the optimum level for long-term production. Fisheries scientists often advocate using decision rule with some "conservation threshold", expressed as a minimum biomass or minimum ratio $R_{cutoff} = B_t/B_0$, below which it is considered best to stop fishing entirely until the stock has recovered to a more productive level (Smith et al. 1993; NRC 1997). Below, I provide limited evaluation of the impact of alternative choices for R_{cutoff} on the loss measures (eqs. 3*a* and 3*b*).

To summarize, many alternative decision rules for regulating quotas during development in relation to probabilistic stock size assessments can be represented as alternative choices for the policy variables $R(t)$, ξ, R_{min}, R_{max}, and R_{cutoff}. The $R(t)$ regulates the acceptable rate of development relative to long-term optimum fishing rate F_{opt}. The ξ sets an acceptable probability for short-term overfishing ($C_t/B_t >$ optimum for year t only). The R_{min} and R_{max} set minimum and maximum ratios of fishing rate F_t to the optimum rate $R(t)F_{opt}$. The R_{cutoff} defines a biomass ratio B_t/B_0 such that the fishery will be closed if there is a probability of ξ or larger that the actual ratio is smaller than this ratio.

Simulation method for comparing policy options

A relatively simple simulation procedure can be used to estimate the loss functions (eqs. 3*a* and 3*b*). Define a grid of B_0 values over the range B_{min} to B_{max}. For each B_0, calculate the reference catch trajectory $C_{opt}(t)$ and then perform a set of time simulations $t = 1,..., T$, with each simulation having random choices for β (uniform over the range β_{min} to β_{max}) and v_t (normal with mean 0 variance 1.0, possibly autocorrelated to represent mixed process/observation error effects). For each simulated year t, (*i*) generate an abundance index Y_t from eq. 4 and use this in eqs. 5–9 to provide an updated estimate of the probability distribution for B_t, the ξ C-risk biomass $B_\xi(t)$, and the associated quota C_t, (*ii*) apply this C_t in the state dynamics relationships (eqs. 10–13) to provide updated conditional predictions $B_{B(0)}(t + 1)$ for all B_0 grid values (including the "true" value chosen for the simulation), and (*iii*) update estimated losses (eqs. 3*a* and 3*b*). Average the summed losses over trials to provide loss curves like Fig. 1, and average these over the prior probability distribution for B_0 to provide expected loss or risk for whatever $R(t)$, ξ, R_{min}, R_{max}, and R_{cutoff} policy is being evaluated.

It only takes around 10 simulation trials for each B_0 to provide quite stable estimates of the loss "profiles" L_{abs} and L_{rel} versus B_0, provided $T \geq 20$. For 10 trials and $T = 20$, each profile takes less than a minute to compute with a Pentium PC. (Computing speed is an important consideration if many policy options ($R(t)$, ξ, R_{min}, R_{max}, and R_{cutoff}) are to be compared.) The procedure described above could be readily extended to represent somewhat more complex assessment methods such as use of Kalman filtering (Pella 1993; Schnute 1994) to provide better conditional estimates B_t given B_0 for situations where there is high process (recruitment) variation. However, I believe it is unlikely that such assessment methods will provide much more precise estimates of B_t than the method defined by eqs. 5–9, unless there is some method (as yet undiscovered) for providing really precise independent estimates of the recruitment anomalies w_t.

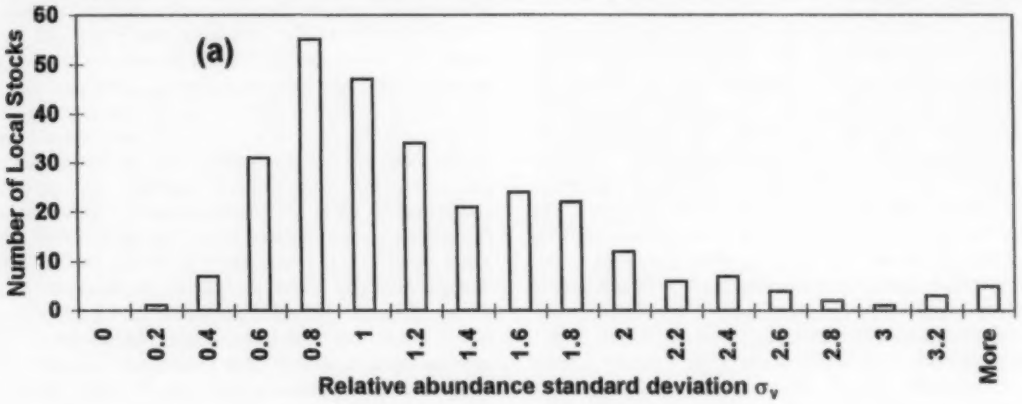
Results

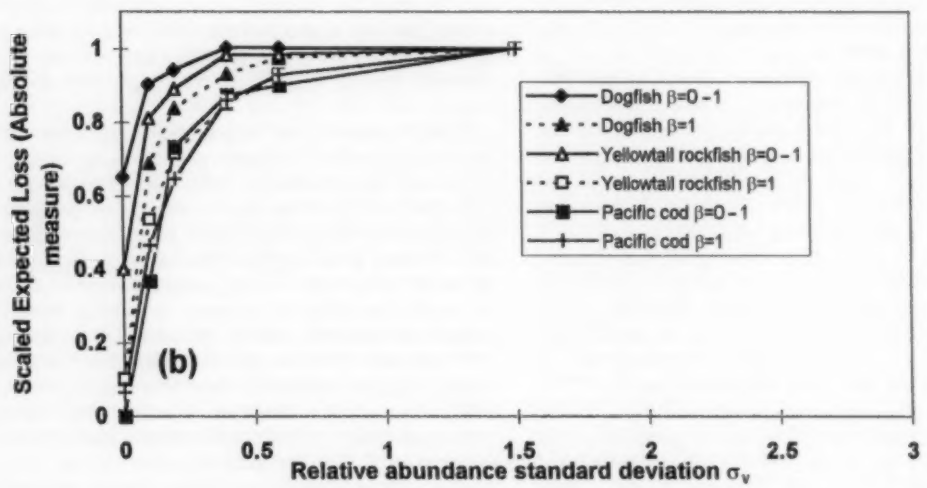
I applied the closed-loop simulation procedure described above to a variety of British Columbia groundfish stocks for which there are developing trawl fisheries and that vary widely in longevity (F_{opt} ranging from 0.035 for spiny dogfish (*Squalus acanthias*) to 0.25 for Pacific cod (*Gadus macrocephalus*)). These patchily distributed, mainly long-lived species are quite representative of developing fisheries today, having escaped earlier attention by fishers for economic or technological (e.g., extreme depth) reasons. They are also typical of modern development situations in that existing trawl capacity is large enough to quickly generate high fishing mortalities, and a species-area quota management system was initiated in 1997 to manage the fishery better.

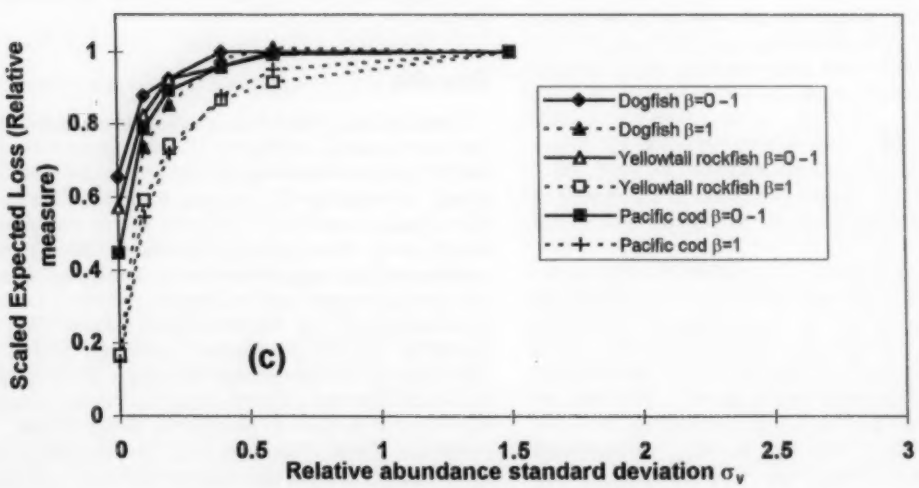
For the British Columbia data, patchy distributions and rapid changes in trawl targeting methods are reflected in typ-

© 1998 NRC Canada

Fig. 2. Frequency distribution of measured standard deviation of relative abundance indices (σ_v) for (*a*) British Columbia groundfish stocks compared with (*b* and *c*) simulated effect of increasing σ_v on expected 20-year loss for three British Columbia stocks representing a range in productivity and longevity: (*b*) absolute expected loss measure; (*c*) relative expected loss measure. Dotted lines show expected loss patterns if the relative abundance index is known to be proportional to biomass (= 1), while solid lines show







© 1998 NRC Canada

higher loss expected if the abundance index may be hyperstable (β anywhere between 0 and 1 with equal probability). Each expected loss estimate was evaluated at best (minimum loss) choice for the overfishing risk probability ξ.

ically variable catch rate and survey abundance index data; based on fitting time series for various stocks to catch rate data using eqs. 5–13, σ_v values range from around 0.2 to over 3.0 (Fig. 2). Note that even the minimum σ_v in Fig. 2 is near the upper end of the range of observation error used in some recent evaluations of stock assessment methods based on relative abundance data (e.g., Polacheck et al. 1993; Chen and Andrew 1998). I have assisted with stock assessments for dozens of developing fisheries around the world, particularly in Mexico and Australia, and on the basis of this experience, I consider the σ_v pattern in Fig. 2 to be quite representative of developing fisheries in general. Values of $\sigma_v < 0.2$ give good visual fits to data, but are uncommon in development practice (Stanley 1992).

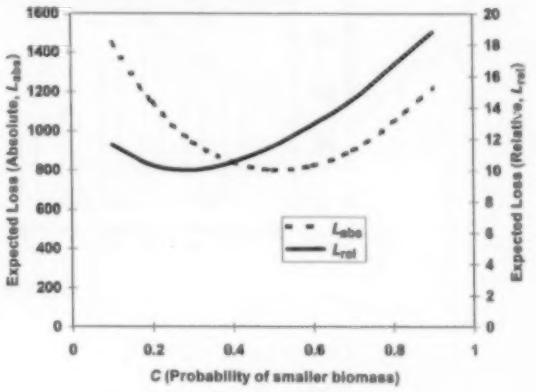
Figure 2 presents the most disturbing finding of this study. For a typical assortment of the British Columbia stocks, it shows how the minimum expected 20-year loss from eqs. 3*a* and 3*b*, averaged over prior probability distributions $P_0(B_0)$, varies with the abundance index standard deviation σ_v. Here the minimization is over choices of the acceptable overfishing probability ξ, so the results are optimal with respect to that policy choice. For these tests, I used a relatively rapid development objective ($t_h = 3$ years in eq. 2). The minimum risk ξ was found to be around 0.5 for L_{abs} in all cases examined and to be between 0.1 and 0.3 for L_{rel} for all cases, i.e., it is best to use certainty equivalent quota choices to minimize absolute loss but very risk-averse quota choices to minimize relative loss (as expected). Typical patterns of variation in expected loss with ξ are shown in Fig. 3; generally the "optimum" value of ξ is quite well defined once a choice between L_{abs} and L_{rel} has been made. The best choice of ξ is not sensitive to development rate as measured by t_h.

The disturbing result in Fig. 2 is that expected loss rises very quickly with σ_v, from a minimum set by how much damage can be done in even the first few years before any index data become available to a maximum where data gathered over the 20 years are so noisy as to have little impact on ability to reduce loss through improved assessment of B_t. Almost all of this increase in loss occurs over a range of σ_v less than even the minimum found in the British Columbia catch rate data; in other words, the catch rate and survey data that have been available so far are not good enough to have any significant impact on expected loss over the next 20 years.

The pessimistic pattern in Fig. 2 is not due simply to using too conservative a likelihood function, in particular assuming the possibility of severe hyperstability in relative abundance indices ($0 < \beta < 1$). The dotted loss lines in Fig. 2 show the effect of using simulated survey or carefully screened catch rate data for which it is safe to assume $\beta = 1$. This certainly helps for $\sigma_v < 0.5$, i.e., the dotted loss lines are well below corresponding lines calculated with $0 < \beta < 1$. But for the majority of the stocks for which σ_v are shown in the top panel, even knowing $\beta = 1$ would not make a substantial difference to expected loss.

The main reason why expected loss during development increases so rapidly with σ_v is that noise in the relative

Fig. 3. Variation in expected loss, averaged over the prior probability distribution for unfished biomass B_0, with choice of the overfishing risk probability ξ. The quota was calculated each year from the optimum fishing mortality rate for that year times the biomass estimate for which the probability was ξ that true biomass was lower than the estimate.



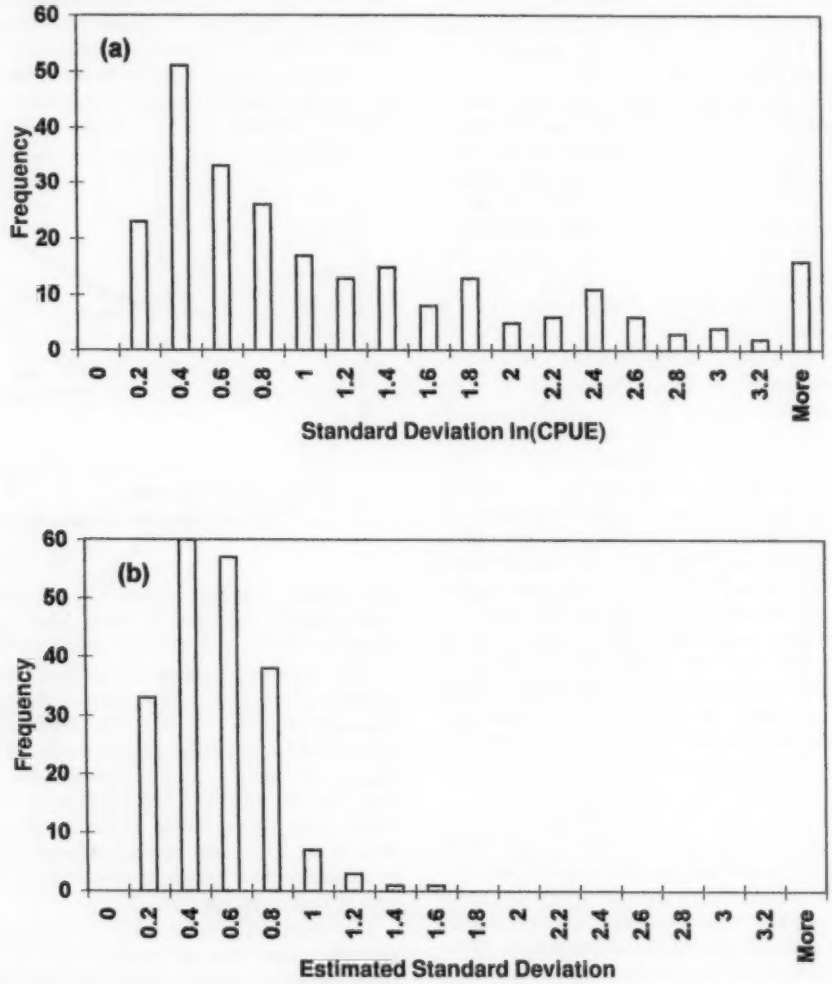
abundance indexing system causes delays in correctly estimating B_0 and hence B_t. Such delays can have a large cumulative effect on B_t through incorrect C_t choices.

This observation leads immediately to a question about whether to use a more "forgiving" loss measure, such as one proportional to $|B_\xi(t) - B_t|$ rather than to $|B_\xi(t) - B_{opt}(t)|$, i.e., ignore cumulative effect of past errors on the difference $B_t - B_{opt}(t)$. We could use such measures for development planning, but we would in effect be saying "it is acceptable to make large quota setting errors early in development, so long as we eventually manage whatever B_t is left wisely." It is doubtful that conservation-oriented stakeholders would accept such arguments.

The distribution of σ_v in Fig. 2 is based on crude catch per effort data that are "contaminated" with process error (recruitment variation) effects and have not been subject to spatial analysis based on accurately georeferenced logbook catches. Figure 4 shows a distribution of σ_v estimates for the same British Columbia stocks but calculated from interannual variation in spatial mean catch rate from detailed logbooks ("exact" georeferences for every shot) that are available for 1994–1996 (around 18 000 shots per year). For each stock each year, the spatial mean catch rate was calculated by assigning shots to 1 square nautical mile grid blocks or strata and then taking the best estimate for each block to be an inverse-distance weighted average of the shot observations for the block and neighboring blocks within 3 nautical miles (Walters and Bonfil 1999). The details of this spatial statistics procedure are not of concern here; the point of Fig. 4 is that substantial variance reduction may be possible by "filtering" fishery data so as to correct for variations caused by changes in spatial distributions of fish and fishing effort, implying considerable value for management of insisting on detailed logbook reporting even in developing

© 1998 NRC Canada

Fig. 4. (*a*) Frequency distribution of measurement error standard deviation (σ_v) estimates for British Columbia groundfish stocks, based on spatial analysis of CPUE data from detailed 1994–1996 logbooks. Interannual variation in spatial mean CPUE is shown only for long-lived stocks that are likely to have had stable biomass over the 3-year period. (*b*) Variation in estimated σ_v expected by chance alone for such short time series.



fisheries. Results like Fig. 2 provide a direct way to estimate this value.

Another way to reduce apparent σ_v in situations like British Columbia groundfish is to aggregate the data over larger spatial areas; this practice usually results in smoother trends to which tighter model fits can almost always be obtained. It is a justifiable practice for highly migratory and dispersive species, but for relatively sedentary species, it can mask a variety of nonsustainable pathologies like sequential depletion of local substocks.

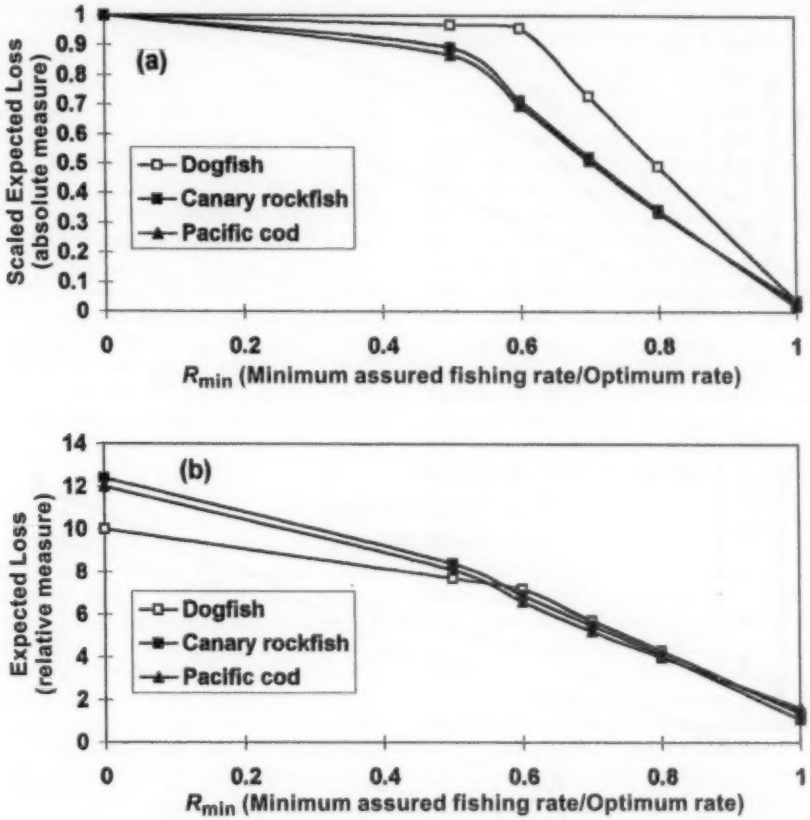
Narrowing the initial range of uncertainty: surveys to establish proven potential

Suppose fishers (or the public) were convinced to invest in an annual survey aimed at providing a minimum density estimate $(B/A)_{min}(t)$ and a minimum estimate of the area $A_{min}(t)$ currently occupied at density $(B/A)_{min}$. A "floor" quota could then be set at $R(t)F_{opt}B_{min}(t)$ with $B_{min}(t) = R_{min}B_t$, overriding the quota calculated from $B_\xi(t)$ in years when $B_{min} > B_\xi$. Without asking whether it would be economical to survey so as to achieve high R_{min} (approaching 1.0), we can at least ask the question how big would R_{min} have to be to make substantial difference to expected loss during development. Figure 5 shows the effect of R_{min} on expected minimum loss for three representative British Columbia groundfish stocks, where as in Fig. 2 the minimum loss presented is with respect to choice of the overfishing risk ξ. Increasing R_{min} causes the optimum ξ to decrease, since there is no "cost" to using a more conservative ξ when surveys will assure that unduly low $B_\xi(t)$ estimates will not be used in quota setting.

Figure 5 implies that surveys to demonstrate minimum biomass are likely to have little impact on expected loss dur-

© 1998 NRC Canada

Fig. 5. Variation in expected loss, averaged over the prior probability distribution for unfished biomass and evaluated at best overfishing risk ξ, with increases in R_{min}, a minimum assured ratio of fishing rate each year to the optimum rate for that year. Higher values of R_{min} represent larger investments in surveys aimed at "proving" a minimum biomass (e.g., $R_{min} = 0.5$ means that surveys have demonstrated biomass to be at least 50% of its actual value). (*a*) Absolute loss measure; (*b*) relative loss measure.



ing development unless such surveys are intensive (accurate *B*/*A*) and extensive (*A* covered) enough to "prove" at least 50% of the actual stock size B_t. This is not a promising result, since it is unusual in fisheries to have density estimation methods capable of guaranteeing to see even half the fish (e.g., higher but unknown proportions typically escape survey trawls), and there is usually considerable ambiguity about the area occupied *A* (especially for parts of the stock range that are large but are occupied at low or very erratic densities). However, at least it is useful to know what standards that surveys for minimum stock size would have to meet in order to substantially reduce expected loss.

Effect of setting upper bounds on fishing mortality with marine protected areas

At the opposite extreme from surveys for proven production potential, suppose fishery regulators elect to close large enough areas during the development so as to insure that fishing mortality rate F_t cannot exceed $R_{max}F_{opt}$. The question then becomes how small would R_{max} have to be in order to substantially reduce expected loss during development. Note that if F_{opt} is small in the first place (e.g., around 0.05 for many long-lived rockfish in British Columbia), then even guaranteeing $R_{max} = 2$ ($F < 0.1$) might have to involve closing 90% of the grounds to fishing every year.

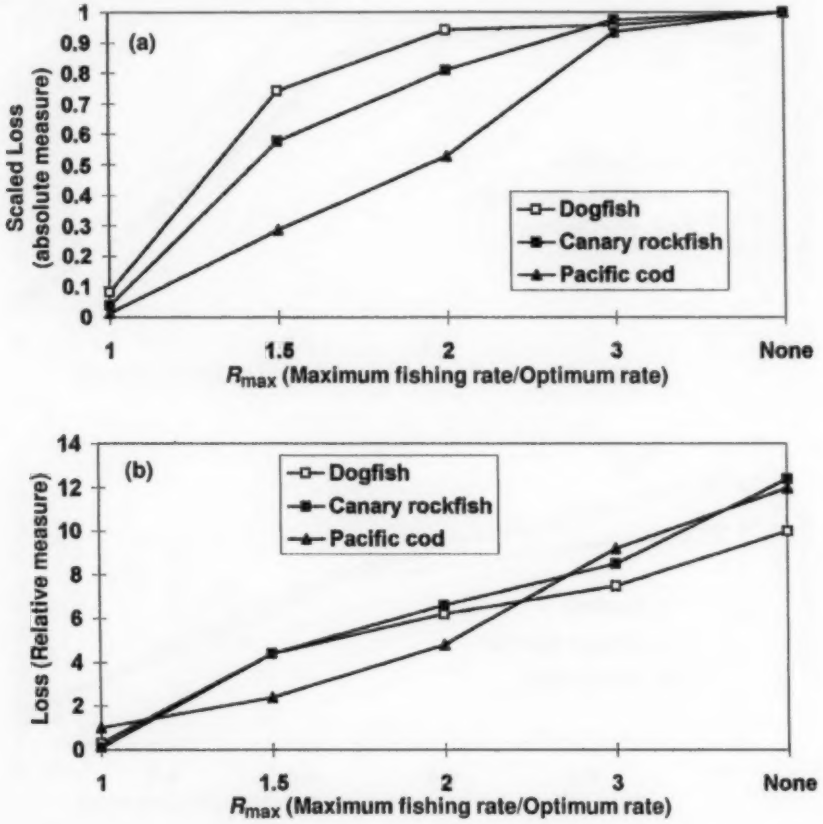
If $R_{max} = 1$, closed areas "guarantee" that fishing mortality rate cannot exceed optimum, and the only losses as measured by eqs. 3*a* and 3*b* can be due to setting an unnecessarily low fishing rate by basing quota decisions on a low-ξ biomass estimate. Hence, for R_{max} near 1.0, the best ξ policy is $\xi = 1.0$, i.e., ignore the probability distribution for biomass B_t. Then as R_{max} is increased (progressively larger open areas that could allow F_t to exceed F_{opt} by progressively larger proportions), the optimum ξ decreases and expected loss evaluated at the best ξ increases (Fig. 6). The pattern of increase is not sensitive to stock productivity characteristics or loss measure, and a robust prediction is that R_{max} exceeding 3.0 (areas open to fishing large enough to allow $F > 3F_{opt}$ in event of bad a overestimate of biomass) provides essentially no protection in terms of reduction in expected loss. In short, the results in Fig. 6 indicate that marine protected areas must be very large indeed to provide a significant hedge against losses for unproductive stocks.

Is progressive exposure a wise strategy?

There are a variety of reasons for insuring that fisheries

© 1998 NRC Canada

Fig. 6. Variation in expected loss, averaged over the prior probability distribution for unfished biomass and evaluated at best overfishing risk ξ, with increases in R_{max}, a maximum assured ratio of fishing rate each year to the optimum rate for that year. Assuring low R_{max} values would generally have to involve large closed areas (exposing only a low proportion of the stock to risk of capture). (*a*) Absolute loss measure; (*b*) relative loss measure.



develop slowly ($R(t)$ increases slowly toward 1.0), beyond just making sure that assumptions of equilibrium catch–effort models are not violated too badly. Is slowing down development sufficient to insure that enough data are gathered for reliable assessment of B_t, without incurring unacceptable losses along the way? Absolute loss as defined in eq. 3*a* certainly is reduced by reducing $R(t)$, whether or not accurate assessment ever becomes possible (lower catch goals mean lower absolute loss in general). But can the relative or "ecological" loss be reduced substantially by slowing development? To answer these questions, I ran a series of expected loss calculations for the same British Columbia stocks as in Figs. 5 and 6, assuming relatively uninformative relative abundance data ($\sigma_v = 0.5$, $\beta = 0$–1) while varying t_h in the calculation of $R(t)$. I also tried using two distinctive values for t_h: a base "stakeholder concensus" value for assessment of $C_{opt}(t)$ and a larger (more conservative, slower development) value for calculation of annual simulated quotas. For all cases, I sought the minimum expected loss achievable over choices of the overfishing risk ξ.

I found no evidence of substantial decrease in expected relative loss (L_{rel}) from slowing development (high t_h) or from using a more conservative t_h for annual quota setting than for setting the reference catch development trajectory. For the more productive stock examples (Pacific cod, canary rockfish (*Sebastes pinniger*)), there was a very slight decrease (3%) in L_{rel} for slower development and a similar slight decrease in L_{abs} for larger t_h values. Increasing t_h generally causes the best choice of ξ to increase (no gain from being doubly conservative). Increasing the time planning horizon ($T = 40$ years instead of 20 years) did not reveal more substantial long-term benefits of initial caution in development. There are at least two reasons for these discouraging results: (*i*) slowing development slows the process of learning about B_0, quite a different effect than slowing development in order to avoid violating equilibrium assumptions of catch–effort assessment methods, leading to larger average errors in quota setting later in development and (*ii*) increasing "opportunity loss" due to taking lower quotas than would (on average) be safe (slow development does reduce odds of immediate overfishing for low B_0, but also leads to underfishing for higher B_0 values).

Is it critical to have a conservation limit B_t/B_0 below which fishing is stopped?

A potentially contentious issue in planning is whether to

© 1998 NRC Canada

include a contingency rule for stopping the fishery in the event that assessment methods indicate high odds that B_t/B_0 is too small. While it would seem only responsible to stakeholders concerned with conservation to make sure that planning is "up front" about this contingency, other stakeholders may misinterpret discussions about such rules as an attempt to sneak unnecessary closures into the plan.

Using the same stocks and measurement assumptions as in the previous subsections, I tested the effect on expected loss of various values between 0 and 0.5 for the cutoff ratio $R_{cutoff} = B_\xi(t)/B_\xi(0)$ below which simulated quota was set to 0. Somewhat surprisingly, R_{cutoff} values > 0 generally resulted in increasing loss by both the absolute and relative measures. The increasing loss occurs because there is a good chance that any particular application of the rule (at any particular time t, risk level ξ) will be the incorrect thing to do (set C_t to zero when it need not be), and such losses more than compensate for instances when relief from fishing helps put the stock "back on track" (nearer the optimum biomass trajectory $B_{opt}(t)$). Hence, it may be unwise to risk stakeholder distrust by putting much planning emphasis on good choice of R_{cutoff}.

Discussion

There are two very different viewpoints about investment in information gathering during fishery development. One is that information gathering should roughly recapitulate the history of stock assessment modeling: start first with catch–effort data and models and then move toward more detailed age-structured analyses. This view is justified by the idea that some development should occur to prove economic potential, before substantial research and assessment are justifiable. The opposite viewpoint is that the most important scientific investments, in analysis of productivity (F_{opt}), bounds for biomass, and sound indices of relative abundance, are most important at the outset of development (e.g., FAO 1995). This paper has concentrated mainly on predictions about performance of the second approach because we have much experience in fisheries that suggests that the first approach is unreliable and because the sort of slow, progressive, and relatively "safe" economic development that it assumes is just not how modern fisheries develop. The second view also reflects the frustration that many of us have felt when working with the "one-way trip" data obtained during typical historical developments (Hilborn and Walters 1992), where assessment results can be highly sensitive to the first few data points, which we usually cannot trust.

Losses can be large during fishery development, even if development is "front loaded" with investment in research to provide biomass bounds and a good estimate of the optimum fishing rate. The value of initial investment can be negated by inadequacy of trend index data used for ongoing assessment. Still, potential for high loss should not be used as an excuse for development to proceed as a free-for-all, with scientists having to base assessments only on crude catch and effort statistics. Management for sustainability is an investment for all concerned (Troadec 1989).

It is particularly worrisome that for many fisheries, there may be no practical way to reduce σ_v into the 0.1–0.2 range where assessment becomes really helpful at reducing losses. High variance in catch rate and survey series is common even when the data have been carefully analyzed to account for gear effects, spatial density patterns, and other causes of variation in relative abundance. For fisheries that are developing today, unpredictability in spatial distribution and availability to both survey and fishing gear may be the norm rather than the exception (the predictable fishing opportunities have long since been developed). But we also see high σ_v even in apparently well-understood situations like the northern Atlantic cod (*Gadus morhua*) stock off Newfoundland (Hutchings 1996), and coefficients of variation for biomass estimates based on trend data are generally >0.25 (Punt and Butterworth 1993). In some circumstances, it may be possible to substantially reduce losses by using age-structured data and assessment methods (NRC 1997; Punt 1997), but even these methods are vulnerable to high σ_v and $\beta \neq 1.0$ (Patterson and Kirkwood 1995).

Could it be that the rather dismal track record of fisheries assessment and management worldwide is due at least in part to not recognizing the fundamental weaknesses in assessment information suggested by Fig. 2? Certainly the published literature on fisheries assessment methods has been highly selective; we tend to publish case examples with relatively low random variation, where the methods at least appear to work. Has this selective process led fisheries managers to expect too much from our assessments and to assume that the methods have been working when in fact they have contributed to overfishing by providing excuses not to take precautionary measures like large marine protected areas? Particularly in relation to quota management, it certainly does not appear that fishery managers have yet started to heed warnings like Walters and Pearse (1996) about the dependence of output control performance on stock assessments and the difficulty (and expense) of obtaining accurate enough assessments to make output controls effective.

The most disappointing results above are not those about risk of poor assessment performance, but rather about efficacy of measures to reduce impact of assessment errors (surveys for proven production potential R_{min}, protected areas to limit fishing mortality R_{max}, and contingency plans for severely depleted situations R_{cutoff}). Unless innovative methods to reduce survey costs are found, it may be unusual for fishery stakeholders to invest enough to insure $R_{min} > 0.5$. Likewise, protected areas and related measures severe enough to insure $R_{max} < 3.0$ are not economically palatable, at least for species where F_{opt} is low in the first place. Figures 5 and 6 suggest that it will often be best to invest in improved information gathering for assessment, rather than "backstop" measures.

What should scientists advise fisheries stakeholders about the best investments to make prior to fisheries development? There are two basic options for reducing expected losses due to stock assessment errors: (*i*) spend more before development starts, to narrow the range of possible unfished biomasses (reduce the B_{max}–B_{min} range) and (or) (*ii*) spend more as development proceeds, to provide better indices of change in relative abundance (smaller σ_v) and (or) higher estimates of proven production potential (R_{min}). We could provide much better advice about how to trade off between these assessment investment options if we could better quantify the relationship between B_{max}–B_{min} and exploratory sur-

© 1998 NRC Canada

vey effort and the relationship between routine survey effort and σ_v. Unfortunately, we cannot safely estimate these relationships from statistical quantities like sample size for which unit costs can be readily assessed; variances actually achieved are often larger than expected from such quantities, implying important sources of variation that are not easy to anticipate in survey design (e.g., interannual variation in proportion of stock "exposed" in the survey frame, variation in survey efficiency due to seasonal changes in spatial aggregation patterns).

For developing fisheries on species that are not highly migratory or dispersive, perhaps we should be seeking development policies that make better use of spatial structure and "replication" of local development opportunities so as to treat development as a sequence of local depletion experiments (e.g., Walters and Collie 1989). Many populations consist of relatively isolated subpopulations, and progressive development across such subpopulations can provide much information on parameters like survey catchability without exposing too large a fraction of the overall stock to overfishing risk early in development. The main barrier that needs to be overcome to make such policies practical is in fact an attitude, among fishers and some managers, that freedom of movement and fishing location choice are a basic right.

Acknowledgements

Rob Kronlund (Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C.) and Andre Punt (CSIRO, Hobart, Tasmania, Australia) provided many helpful comments on the manuscript, as did two anonymous reviewers. Financial support was provided from a Natural Sciences and Engineering Research Council of Canada operating grant to the author.

References

Chen, Y., and Andrew, N. 1998. Parameter estimation in modelling the dynamics of fish stock biomass: are currently used observation-error estimators reliable? Can. J. Fish. Aquat. Sci. **55**: 749–760.

Deriso, R.B., Quinn, T.J., II, and Neal, R.P. 1985. Catch–age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. **42**: 815–824.

Engen, S., Lande, R., and Saether, B.-E. 1997. Harvesting strategies for fluctuating populations based on uncertain population estimates. J. Theor. Biol. **186**: 201–212.

FAO (Food and Agricultural Organization of the United Nations). 1995. Precautionary approach to fisheries. Part 1. FAO Fish. Tech. Pap. 350.

Fournier, D., and Archibald, C.P. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. **39**: 1195–1207.

Gavaris, S. 1988. A adaptive framework for the estimation of population size. CAFSAC Res. Doc. 88/29.

Hilborn, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. **36**: 1477–1489.

Hilborn, R., and Sibert, J. 1988. Adaptive management of developing fisheries. Mar. Policy, **12**: 112–121.

Hilborn, R., and Walters, C. 1992. Quantitative fisheries stock assessment and management: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Ludwig, D., and Walters, C. 1985. Are age-structured models appropriate for catch–effort data? Can. J. Fish. Aquat. Sci. **42**: 1066–1072.

Megrey, B. 1989. Review and comparison of age-structured stock assessment models. Am. Fish. Soc. Symp. **6**: 8–48.

Mertz, G., and Myers, R.A. 1998. A simplified formulation for fish production. Can. J. Fish. Aquat. Sci. **55**: 478–484.

Methot, R.D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. Int. North Pac. Fish. Comm. Bull. **50**: 259–277.

Mood, A.M., and Graybill, F.A. 1963. Introduction to the theory of statistics. 2nd ed. McGraw-Hill Book Co. Inc., New York.

NRC (National Research Council). 1997. Improving fish stock assessments. National Academy Press, Washington, D.C.

Patterson, K. 1992. Fisheries for small pelagic species: an empirical approach to management targets. Rev. Fish Biol. Fish. **2**: 321–338.

Patterson, K., and Kirkwood, G.P. 1995. Comparative performance of ADAPT and Laurec–Shepherd methods for estimating fish population parameters and in stock management. ICES J. Mar. Sci. **52**: 183–196.

Pearse, P.H., and Walters, C. 1992. Harvesting regulation under quota management systems for ocean fisheries: decision making in the face of natural variability, weak information, risk, and conflicting incentives. Mar. Policy, **16**: 167–182.

Pella, J.J. 1993. Utility of structural time series models and the Kalman filter for predicting consequences of fishery actions. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. *Edited by* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II. Alaska Sea Grant College Program Report No. 93-02. University of Alaska, Fairbanks, Alaska. pp. 571–594.

Polacheck, T., Hilborn, R., and Punt, A.E. 1993. Fitting surplus production models: comparing methods and measuring uncertainty. Can. J. Fish. Aquat. Sci. **50**: 2597–2607.

Punt, A.E. 1997. The performance of VPA-based management. Fish. Res. (Amst.), **29**: 217–243.

Punt, A.E., and Butterworth, D.S. 1993. Variance estimates for fisheries assessment: their importance and how best to evaluate them. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 145–162.

Schnute, J. 1994. A general framework for developing sequential fisheries models. Can. J. Fish. Aquat. Sci. **51**: 1676–1688.

Schnute, J., and Richards, L. 1995. The influence of error on population estimates from catch–age models. Can. J. Fish. Aquat. Sci. **52**: 2063–2077.

Smith, A.D.M. 1993. Risks of over- and under-fishing new resources. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. No. 120. pp. 261–267.

Smith, S.J., Hunt, J.J., and Rivard, D. (*Editors*). 1993. Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. No. 120.

Stanley, R.D. 1992. Bootstrap calculation of catch-per-unit-effort variance from trawl logbooks: do fisheries generate enough ob-

© 1998 NRC Canada

servations for stock assessments? N. Am. J. Fish. Manage. **12**: 19–27.

Starr, P., Annala, J.H., and Hilborn, R. 1998. Contested stock assessment: two case studies. Can. J. Fish. Aquat. Sci. **55**: 529–537.

Troadec, J.-P. 1989. The mutation of world fisheries: its effect on management priorities and practices. *In* Management of world fisheries: implications of extended coastal state jurisdiction. *Edited by* E.L. Miles. University of Washington Press, Seattle, Wash. pp. 1–18.

Walters, C.J. 1986. Adaptive management of fishing systems. Macmillan Publishing Co., New York.

Walters, C.J. 1994. Use of gaming procedures in evaluation of management experiments. Can. J. Fish. Aquat. Sci. **51**: 2705–2714.

Walters, C.J., and Bonfil, R. 1999. Multispecies spatial assessment models for the B.C. trawl fishery. Can. J. Fish. Aquat. Sci. **56.** In press.

Walters, C.J., and Collie, J.S. 1989. An experimental strategy for groundfish management in the face of large uncertainty about stock size and production. Can. Spec. Publ. Fish. Aquat. Sci. No. 108. pp. 13–25.

Walters, C.J., and Ludwig, D. 1994. Calculation of Bayes posterior probability distributions for key population parameters. Can. J. Fish. Aquat. Sci. **51**: 713–722.

Walters, C.J., and Parma, A.M. 1996. Fixed exploitation strategies for coping with effects of climate change. Can. J. Fish. Aquat. Sci. **53**: 148–158.

Walters, C.J., and Pearse, P.H. 1996. Stock information requirements for quota management systems in commercial fisheries. Rev. Fish Biol. Fish. **6**: 21–42.

Walters, C.J., and Punt, A. 1994. Placing odds on sustainable catch using virtual population analysis and survey data. Can. J. Fish. Aquat. Sci. **51**: 946–958.

© 1998 NRC Canada

DISCUSSION

Methods of studying fish feeding: a comment[1]

Sture Hansson

In ecosystem and food web studies, as well as in general biological descriptions, information on diets is of central interest and analyses of stomach contents are frequently done. However, the way in which these analyses are performed varies substantially, which can make it difficult to compare results. From this perspective, Cortés (1997) reviewed methods used in diet studies. One of his conclusions is that the index of relative importance (IRI) should be used as "a standardized measure in dietary analyses." This conclusion is not based on numerical or statistical analyses, and it is difficult to understand exactly why Cortés considers IRI values better descriptors of a diet than other measures. As touched on by Cortés, IRI values can vary depending on the taxonomic resolution in the analysis, but he does not seem to find this critical. In my opinion, this sensitivity actually makes IRI less suitable than suggested by Cortés, and in fact, I argue that it should be avoided or even abandoned.

Below, the weakness of the IRI will be illustrated by comparing different analyses of the same set of diet data. The equations that the analyses are based on are

$$\mathrm{IRI} = \%O_i(\%W_i + \%N_i)$$

and

$$\%\,\mathrm{IRI}_i = \frac{100 \times \mathrm{IRI}_i}{\sum_{j=1}^{n} \mathrm{IRI}_j}$$

where i is one of j different prey types, $\%O_i$ is its frequency of occurrence (i.e., the proportion of the analysed fish that held prey i) and $\%W_i$ and $\%N_i$ are the proportions of the stomach content by weight and by number, respectively, made up by prey i.

In the first of the analyses (Table 1), a high taxonomic resolution is used, and the other analysis is made after merging five different prey species into one group (low taxonomic resolution; Table 1). To further illustrate the sensitivity of IRI to the taxonomic resolution, Fig. 1 shows how a diet based on this index changes with the successive merging of prey. When merging prey, I assumed that some stomachs contained more that one of the prey species concerned, which made it impossible to just add $\%O$ values. When two prey species were merged, each with the occurrence of 25%, their combined $\%O$ was set to 40%. When merging three, four, and five prey, the corresponding occurrence values were set to 60, 80, and 100%. It is acknowledged that these assumptions influence the results; however, they are not unrealistic, and if IRI should be used as a "standardized measure in dietary analyses," its properties should allow these assumptions.

Table 1. Hypothetical results from a single stomach content study, with alternative taxonomic resolutions.

	$\%W$	$\%N$	$\%O$	%IRI
High taxonomic resolution				
Prey species 1	10	10	25	10
Prey species 2	10	10	25	10
Prey species 3	10	10	25	10
Prey species 4	10	10	25	10
Prey species 5	10	10	25	10
Prey species 6	10	10	25	10
Prey species 7	10	10	25	10
Prey species 8	10	10	25	10
Prey species 9	10	10	25	10
Prey species 10	10	10	25	10
Summed for prey species 1–5				50
Summed for prey species 6–10				50
Low taxonomic resolution				
Prey species 1	10	10	25	4
Prey species 2	10	10	25	4
Prey species 3	10	10	25	4
Prey species 4	10	10	25	4
Prey species 5	10	10	25	4
Prey species 6–10	50	50	100	80
Summed for prey species 1–5				20
Summed for prey species 6–10				80

The IRI results are strongly influenced by the prey categories applied. When taxonomic resolution is increased for a group of prey, IRI predicts a decreased importance of this group in the diet. This is clearly seen from Fig. 1 and a comparison between "summed for prey species 6–10" for the two resolution levels in Table 1. Furthermore, the taxonomic resolution in one group of prey also influences the predicted significance of other prey. In the example given in Table 1, merging prey species 6–10 reduced the contribution of species 1–5 is to less than half.

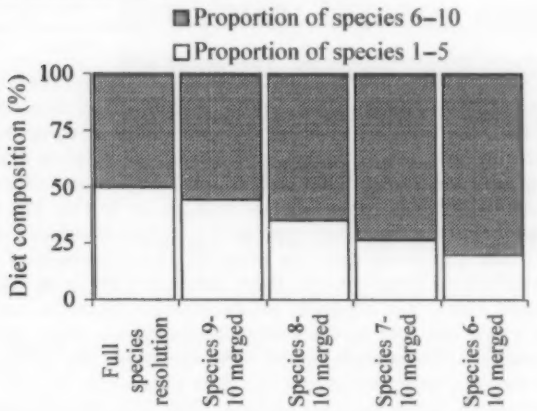
Received March 11, 1998. Accepted September 17, 1998. J14482

S. Hansson. Department of Systems Ecology, Stockholm University, S-106 91 Stockholm, Sweden. e-mail: sture.hansson@system.ecology.su.se

[1]Comment on review by E. Cortés. 1997. Can. J. Fish. Aquat. Sci. **54**: 726–738.

© 1998 NRC Canada

Fig. 1. Effects of different degree of merging of prey when using the %IRI method to analyze a single hypothetical diet data set. The diets referred to as "full species resolution" and "species 6–10 merged" are identical with "high resolution" and "low resolution" in Table 1, respectively.



This problem with IRI is not just theoretical but can be highly relevant in practice. For example, if zooplankton is a target group in a diet study, the number of prey groups can then be substantial if these prey are separated among species and furthermore among nauplii and copepodite stages, sexes, and females with and without eggs. A consequence of careful separation of zooplankton into such groups, if IRI is used, is that the general importance of zooplankton decreases relative to other prey types. Clearly, an index that presents the dietary importance of a prey category as being smaller when studied in greater detail cannot be recommended for use in scientific studies.

In an earlier paper, Macdonald and Green (1983) argued against compound indices like IRI, because they may be redundant and add little new information compared with the separate components alone. In addition, the simple analysis presented above shows that IRI is a basically unsound index. Concerning IRI, Cortés (1997) suggests that "By incorporating bulk, amount, and occurrence into a single measure it appears to provide a more accurate description of dietary importance." It is not clear what Cortés actually means with "dietary importance," but I argue that the IRI method is potentially misleading. In my opinion, the method best suited for diet analyses depends on the questions asked. For example, if we are interested in energy flow in food webs, $\%W_i$ values are relevant (possibly after adjusting energy densities and prey specific differences in gut evacuation rates), while $\%N_i$ values combined with in situ abundances of different prey suit the purpose if we are asking questions about prey preferences.

References

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can. J. Fish. Aquat. Sci. **54**: 726–738.

Macdonald, J.S., and Green, R.H. 1983. Redundancy of variables used to describe importance of prey species in fish diets. Can. J. Fish. Aquat. Sci. **40**: 635–637.

© 1998 NRC Canada

Methods of studying fish feeding: reply[1]

Enric Cortés

Dietary descriptions of fish and other aquatic vertebrates are greatly influenced by the choice of the method used to quantify the relative importance or contribution of each prey type to the diet. This is because the most commonly used measures (numerical abundance, frequency of occurrence, and volume or weight measures) convey different types of information on feeding habits (Macdonald and Green 1983; Bigg and Perez 1985; Cortés 1997). This limitation of single indices led Pinkas et al. (1971) to propose the index of relative importance, or IRI, a compound index that describes the relative contribution of stomach contents to the diet. In a recent paper (Cortés 1997), I proposed to include the IRI standardized to 100% (%IRI), in addition to reporting the three single measures, *to facilitate comparisons between dietary studies*. Hansson argues that the IRI should be abandoned overall because it underrepresents lower taxonomic categories as shown in a hypothetical example.

Some of the limitations and biases of the single measures and some compound indices have been discussed elsewhere (Pinkas et al. 1971; Hyslop 1980; Macdonald and Green 1983; Bigg and Perez 1985). I argued that all three single measures should be reported when attempting to describe diets of populations or species because use of only one or two of them can be misleading (Fig. 2*b* in Cortés 1997 illustrates this point). Ideally, energy value of the prey should also be included as a measure of dietary importance, but this is beyond the scope of most studies. In his comment, Hansson shows that the IRI has limitations when attempting to quantify stomach contents from a single study because of the multiplicative effect that *%O* has on the index, with the net result of underestimating the contribution of those prey species identified to a lower taxonomic level. Although this is a valid point, I contend that the value of *%O* used in his example greatly influences the outcome, as recognized by Hansson. Before completely ruling out the use of IRI in dietary studies, its suitability and, by extension, that of all compound indices should be investigated further with examples drawn from multiple real data sets. As also pointed out by Hansson, conclusions should be based on numerical or statistical analyses, rather than on personal preferences or limited testing of hypothetical examples.

My recommendation of using %IRI responded more to a need to promote consistency and facilitate comparisons (Cortés 1997) than to a strong advocacy for compound indices. Indeed, I proposed to depict all three single measures graphically to easily visualize the importance of each food category in stomach content analyses. However, when making intra- or inter-specific comparisons, such as in calculations of dietary overlap, dietary breadth, or trophic levels, use of %IRI as a standardized measure can be useful despite the bias associated with this measure. In my opinion, it is preferable to using a single index because %IRI is an individual metric that integrates all three single measures, each of which can lead to misleading interpretations when used separately. For example, use of %N only to describe the diet of the blue shark would give the false impression that crustaceans are by far the most important item (Fig. 2*b* in Cortés 1997). In contrast, %IRI also considers contributions in weight and occurrence, thus emphasizing more the importance of cephalopodian molluscs and teleost fishes in the diet, which is more accurate (as determined in numerous studies of blue shark diets). Furthermore, if another study of blue shark diet were to use only %O or %W, for example, comparisons would be hindered because %N and %O or %W are not directly comparable. By combining the three single indices, %IRI puts results into a common metric, more amenable for use in diet comparisons and calculation of other trophic measures.

References

Bigg, M.A., and Perez, M.A. 1985. Modified volume: a frequency–volume method to assess marine mammal food habits. *In* Marine mammals and fisheries. *Edited by* J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen &Unwin, London, U.K. pp. 277–283.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can. J. Fish. Aquat. Sci. **54**: 726–738.

Hyslop, E. J. 1980. Stomach contents analysis: a review of methods and their application. J. Fish. Biol. **17**: 411–429.

Macdonald, J.S., and Green, R.H. 1983. Redundancy of variables used to describe importance of prey species in fish diets. Can. J. Fish. Aquat. Sci. **40**: 635–637.

Pinkas, L.M., Oliphant, S., and Iverson, I.L.K. 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. Calif. Fish Game, **152**: 1–105.

Received June 24, 1998. Accepted July 24, 1998.
J14665

E. Cortés. Institute for Fishery Resource Ecology, National Marine Fisheries Service, and Florida State University, 3500 Delwood Beach Road, Panama City, FL 32408, U.S.A. e-mail: cortes@bio.fsu.edu

[1]Reply to comment by S. Hansson. 1998. Can. J. Fish. Aquat. Sci. **55**: 2706–2707.

© 1998 NRC Canada

ERRATA

Erratum: Winter mortality of young-of-the-year Hudson River striped bass (*Morone saxatilis*): size-dependent patterns and effects on recruitment

Thomas P. Hurst and David O. Conover

Ref: Can. J. Fish. Aquat. Sci. **55**: 1122–1130 (1998).

In Fig. 1*a*, an r^2 value of 0.755 and a p value of 0.226 are given. The correct values should be $r^2 = 0.233$ and $p = 0.226$.

Accepted December 3, 1998.
J13673E

T.P. Hurst[1] and D.O. Conover. Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, U.S.A.

[1]Author to whom all correspondence should be addressed. e-mail: hurst@msrc.sunysb.edu

© 1998 NRC Canada

Erratum: Comparison of methods to account for autocorrelation in correlation analyses of fish data

Brian J. Pyper and Randall M. Peterman

Ref: Can. J. Fish. Aquat. Sci. **55**: 2127–2140 (1998).

Equation 2 (p. 2128) is incorrect. The equation should read as follows:

$$r_{crit} = \sqrt{t^2_{\alpha,N^*}/(t^2_{\alpha,N^*} + N^*)}$$

Also, the parenthetic statement in the second sentence of the second paragraph of the Appendix (p. 2140) should read: "...(with first-order autoregressive parameters ϕ_{I_x}, ϕ_{I_y}, and ϕ_C, respectively),..."

Accepted December 3, 1998.
J14211E

B.J. Pyper[1] and R.M. Peterman. School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.

[1]Author to whom all correspondence should be addressed. e-mail: pyper@sfu.ca

© 1998 NRC Canada

ASSIGNMENT OF COPYRIGHT

Ms. No. _____

To: NATIONAL RESEARCH COUNCIL OF CANADA ("NRC") Research Press

From: _____

_____

_____

_____

(name and address of author signing this form)

This refers to the manuscript entitled: _____

_____

written by myself and the following additional author(s): _____

_____

for publication in: _____

1. I declare that the list of authors fairly conforms to academic conventions about who should be listed. I declare that the manuscript, or its equivalent, has not been submitted for publication elsewhere. If it is accepted for publication by the National Research Council of Canada, I will ensure that it, or its equivalent, is not submitted for publication elsewhere.

2. I declare that I am (check ONE):

☐ (a) the sole owner of the copyright relating to the manuscript,	and →	I **assign** to NRC the entire copyright.
☐ (b) a part owner of the copyright, in conjunction with interests held by co-authors or their employers,	and →	I **assign** to NRC my entire interest in the copyright, and I expect the co-authors to also sign a form like this one.
☐ (c) an agent of my employer with authority to assign the copyright owned by the employer, who is: _____,	and →	I **assign** to NRC, on behalf of my employer, my employer's entire interest in the copyright relating to the manuscript, and I expect the co-authors to also sign a form like this one.
☐ (d) a public servant in Canada (federal, provincial or territorial) or the United Kingdom, so that the copyright is owned by Her Majesty,	and →	I have obtained the approval of my employer, according to the terms of my employment, to grant NRC **non-exclusive permission** to publish the manuscript and administer the copyright.
☐ (e) a public servant of the United States of America, and subject to the law that creates no U.S. copyright for the manuscript,	and →	I **assign** to NRC, on behalf of my employer, my employer's entire interest in any copyright that may exist outside the U.S., and I expect the co-authors to sign a form like this one.

3. I understand that my submission of this document does not guarantee publication, and that publication will not occur until **all authors** have provided a copyright transfer. If the manuscript is not published within 2 years after I sign this, the assignment is revoked.

Signed at _____ on _____

(City and Province/State) (Date)

_____

(Signature)

[Standard NRC form; alterations not acceptable.]

Comments on Copyright Transfer
(with extracts from the *Copyright Act*, Revised Statutes of Canada 1985, chapter C-42, as amended)

The publisher is not permitted to publish the manuscript without permission or an assignment of ownership of copyright. For greatest flexibility, and to be prepared to deal with future uses of the published material, the publisher requires ownership.

The owner may assign the right, but that assignment must be in writing:

13.(4) The owner of the copyright in any work may assign the right, either wholly or partially, and either generally or subject to territorial limitations, and either for the whole term of the copyright or for any other part thereof, and may grant any interest in the right by licence, but no assignment or grant is valid unless it is in writing signed by the owner of the right in respect of which the assignment or grant is made, or by his duly authorized agent.

The owner may be the author, but in many cases, the owner is the author's employer:

13.(3) Where the author of a work was in the employment of some other person under a contract of service or apprenticeship and the work was made in the course of his employment by that person, the person by whom the author was employed shall, in the absence of any agreement to the contrary, be the first owner of the copyright, but where the work is an article or other contribution to a newspaper, magazine or similar periodical, there shall, in the absence of any agreement to the contrary, be deemed to be reserved to the author a right to restrain the publication of the work, otherwise than as part of a newspaper, magazine or similar periodical.

The only exception to taking ownership arises when the manuscript is covered by Crown copyright owned by a Canadian government.

12. Without prejudice to any rights or privileges of the Crown, where any work is, or has been, prepared or published by or under the direction or control of Her Majesty or any government department, the copyright in the work shall, subject to any agreement with the author, belong to Her Majesty and in that case shall continue for the remainder of the calendar year of the first publication of the work and for a period of fifty years following the end of that calendar year.

Governments, and in particular the federal government, do not have a simple mechanism for assigning ownership of this particular type of Crown asset. Therefore, when an author is a public servant so that there is Crown copyright in the manuscript, a simple permission to use is acceptable to the publisher, if it is granted by a person with appropriate authority.

CESSION DU DROIT D'AUTEUR

Document n° _____

Au : CONSEIL NATIONAL DE RECHERCHES DU CANADA («CNRC») - Presses scientifiques

De : _____

_____

_____

_____

(nom et adresse de l'auteur qui signe le présent formulaire)

La présente cession porte sur le document intitulé : _____

_____

rédigé par moi, en collaboration avec l'auteur/les auteurs suivant(s) : _____

_____

aux fins de publication dans : _____

1. Je déclare que la liste des auteurs ci-dessus respecte les pratiques usuelles de rédaction savante quant aux personnes dont le nom doit être cité. Je déclare que le document ou son équivalent n'a pas été soumis à quelque autre organisme aux fins de publication. Si le CNRC accepte de publier le document, je m'assurerai que celui-ci ou son équivalent n'est soumis à aucun autre organisme aux fins de publication sans en obtenir la permission préalable du CNRC.

2. Je déclare être (UN SEUL choix) :

☐	(a) le seul titulaire de droit d'auteur afférent au document,	et →	je **cède** le droit d'auteur intégral au CNRC.
☐	(b) un titulaire partite du droit d'auteur, de concert avec des coauteurs ou leurs employeurs,	et →	je **cède** ma part du droit d'auteur au CNRC et m'attends à ce que les coauteurs signent une entente comparable.
☐	(c) un agent de mon employeur ayant l'autorité de céder le droit d'auteur appartenant à l'employeur, nommément : _____,	et →	je **cède** au CNRC, au nom de mon employeur, la part entière du droit d'auteur afférent au document appartenant à mon employeur, et m'attends à ce que les coauteurs signent une entente comparable.
☐	(d) un fonctionnaire du Canada (fédéral, provincial ou territorial) ou du Royaume-Uni, donc le droit d'auteur appartient à Sa Majesté,	et →	j'ai obtenu de mon employeur, en vertu de mes conditions d'emploi, l'autorisation d'accorder au CNRC la **permission non exclusive** de publier le document et de gérer le droit d'auteur.
☐	(e) un fonctionnaire des États-Unis d'Amérique, donc sujet à la loi qui n'associe aucun droit d'auteur américain au document,	et →	je **cède** au CNRC, au nom de mon employeur, la part entière de quelque droit d'auteur en vigueur ailleurs qu'aux É.-U. appartenant à mon employeur, et m'attends à ce que les coauteurs signent une entente comparable.

3. Je comprends que la soumission du document ne garantit aucunement sa publication et que la publication ne pourra être réalisée tant que **tous les auteurs** n'auront pas signé une cession du droit d'auteur. Si le document n'est pas publié dans les deux années suivant ma signature des présentes, la cession sera automatiquement révoquée.

Signé à _____, le _____

(ville et province/état) (date)

_____

(signature)

[Formulaire normalisé du CNRC; aucune modification permise]

Commentaires sur la cession du droit d'auteur
(accompagnés d'extraits de la *Loi sur le droit d'auteur*, Lois révisées du Canada 1985, chapitre C-42 modifié)

L'éditeur ne peut publier un document sans la permission ou une cession du droit d'auteur. Pour des raisons de souplesse et en vue de l'utilisation future du document publié, l'éditeur doit devenir titulaire du droit d'auteur.

Le titulaire peut céder le droit, mais cette cession doit être faite par écrit :

13.(4) Le titulaire du droit d'auteur sur une oeuvre peut céder ce droit, en totalité ou en partie, d'une façon générale, ou avec des restrictions territoriales, pour la durée complète ou partielle de la protection; il peut également concéder, par une licence, un intérêt quelconque dans ce droit; mais la cession ou la concession n'est valable que si elle est rédigée par écrit et signée par le titulaire du droit qui en fait l'objet, ou par son agent dûment autorisé.

Le titulaire peut être l'auteur, mais dans plusieurs cas, le titulaire est l'employeur de l'auteur:

13.(3) Lorsque l'auteur est employé par une autre personne en vertu d'un contrat de louage de service ou d'apprentissage, et que l'oeuvre est exécutée dans l'exercice de cet emploi, l'employeur est, à moins de stipulation contraire, le premier titulaire du droit d'auteur; mais lorsque l'oeuvre est un article ou un autre contribution, à un journal, à une revue ou à un périodique du même genre, l'auteur, en l'absence de convention contraire, est réputé posséder le droit d'interdire la publication de cette oeuvre ailleurs que dans un journal, une revue ou un périodique semblable.

La seule exception dans la cession du droit d'auteur est lorsque le document est associé au droit d'auteur de la Couronne, qui appartient au gouvernement du Canada .

12. Sous réserve de tous les droits ou privilèges de la Couronne, le droit d'auteur sur les oeuvres préparées ou publiées par l'entremise, sous la direction ou la surveillance de Sa Majesté ou d'un ministère du gouvernement, appartient, sauf stipulation conclue avec l'auteur, à Sa Majesté et, dans ce cas, il subsiste jusqu'à la fin de la cinquantième année suivant celle de la première publication de l'oeuvre.

Les gouvernements, en particulier le gouvernement fédéral, ne disposent pas d'un mécanisme simple de cession de droit d'auteur pour ce genre de biens de la Couronne. C'est pourquoi lorsqu'un auteur est un fonctionnaire et que, par conséquent, le droit d'auteur appartient à la Couronne, une simple permission d'usage est suffisante pour l'éditeur, pour autant que celle-ci ait été octroyée par une personne jouissant de l'autorité nécessaire pour ce faire.

Canadian Journal of Fisheries and Aquatic Sciences

Author Index
Volume 55, 1998

Journal canadien des sciences halieutiques et aquatiques

Index des auteurs
Volume 55, 1998

Ackman, R.G., 1378
Adams, N.S., 781
Adamson, M.L., 977
Adkison, M.D., 2503
Alexander, J.E., Jr., 220
Allard, J., 246
Allen, H.E., 2221
Alunno-Bruscia, M., 459
Anderson, C.S., 1854
Anderson, J.J., 658
Andren, A.W., 835
Andrew, N., 749
Anema, C., 544
Angus, R.B., 1208
Annala, J.H., 529
Armstrong, J.D., S303
Arnott, S.E., 1573
Atkinson, D.B., 1704
Attayde, J.L., 1789
Atwell, L., 1114
Augustin, N.H., 2608
Azuma, D., 1807
Babiarz, C.L., 835
Baca, R.M., 2087
Baker, E.W., 206
Bakke, T.A., 507, S48, S247
Balk, L., 815
Barbieri, L.R., 2244
Barbin, G.P., 564
Barroso, J.B., 649
Barrowman, N.J., 1466, 1477
Barton, D.R., 1919
Baudin, J.P., 999
Beauchamp, D.A., 1285
Behnke, R.J., S281
Belchier, M., 925
Bennett, S.N., 977
Benoît, H.P., 2425
Benoit, J.M., 835
Berg, N., 1807
Berg, O.K., 47
Bernard, D.R., 1983
Bernatchez, L., 1264, 1739
Bilby, R.E., 1909
Bird, G.A., 987
Bisbal, G.A., 2178
Bisson, P.A., 1909
Blais, A.M., 1078
Blier, P.U., 788
Boisclair, D., 796
Borchers, D.L., 2608
Botsford, L.W., 1236
Boustead, N., 554
Bowen, B.W., 2539
Bowen, W.D., 1378
Boyd, I.L., 845
Bozelli, R.L., 1789
Bradford, D.F., 2478
Bradford, M.J., 2355
Brand, U., 1798
Bremset, G., 47
Bresko, K.L., 220
Bridson, M., 2355
Brodersen, K.P., 1093
Brodeur, J.C., 438
Brodziak, J.K.T., 882
Brooks, E.N., 199, 1477, 2001
Brown, A.D., 2478
Brown, G.E., 611
Brown, G.S., 1524
Brown, J.A., 1307, 1317
Brown, S.K., 1704
Browne, D., 1798
Bryant, M.D., 1285
Buchholz, F., 328, 1997
Buckel, J.A., 1695
Buckland, S.T., 2608
Buja, K.R., 1704
Bukaveckas, B.L., 220
Bukaveckas, P., 958
Burwen, D.L., 2492
Bussières, D., 1068
Butturini, A., 1938
Caissie, D., 485
Campana, S., 1798
Campbell, C.E., 230
Caouette, J., 1503
Caputi, N., 925
Caraco, N.F., 54
Carignan, R., 1078
Carls, M.G., 2300
Carlson, A., 1807
Caron, F., 246
Carpenter, S.R., 387, 1169
Cartwright, M.A., 1285
Casas, M.C., 162
Casey, J.M., 2329
Cavalli, L., 2341
Cech, J.J., Jr., 861
Chang, K.-H., 1864
Chapman, P.M., 2221
Chappaz, R., 2341
Chaput, G., 246
Chen, C.Y., 339
Chen, Y., 749
Chevalet, C., 715
Chouinard, G.A., 2548
Chow-Fraser, P., 150, 1189
Chubb, C., 925
Claflin, L., 1704
Clair, T.A., 2464
Clark, A.-M., 2539
Clark, J.E., 1983
Clarke, E.D., 2608
Clay, C.S., 1296
Clay, D., 2274
Claytor, R.R., 1419
Clifford, S.L., 358
Cluis, D.A., 63
Cobb, J.S., 2436
Cobb, S.E., 28
Cobbs, G.A., 220
Coe, T.A., S267
Comeau, M., 262
Conan, G.Y., 262
Condrey, R.E., 1328
Conover, D.O., 1122, 1149, 1695, 2709
Conrad, R.H., 1395

Note: Page numbers preceded by the letter "S" are articles published in the supplement.

Nota : Les numéros de pages précédés de la lettre S désignent les articles publiés dans le supplément .

Conroy, M.J., 539
Cook, R.M., 1632
Cook, T., 2028
Cooke, S.E., 2292
Cooper, S.D., 2478
Copeman, D., 230
Cordue, P.L., 376, 1682
Coronado, C., 2067
Cortés, E., 2708
Cotter, A.J.R., 1607
Couture, P., 1591
Crane, P.A., 1748
Crivelli, A.J., 737
Croke, S., 1208
Cronberg, G., 1926
Crosbie, B., 1189
Culver, D.A., 2572
Cumming, B.F., 668
Cunjak, R.A., S161, S181, S312
Currie, S., 1208
Cyr, H., 414, 967
Dalet, C., 597
Danzmann, R.G., 1553
Davidson, K., 1208
Davis, B.M., 1140
de la Higuera, M., 649
de la Noüe, J., 2019
Degerman, E., 1034
DeGraaf, R.M., S1, S303
Dempson, J.B., 246, 1264
Desrochers, M., 788
Dickhoff, W.W., 2376
Die, D., 1645
Dobson, E.P., 1131
Dockray, J.J., 1534
Dodson, J.J., 1068, 1663, 1674, 1739, 2662, S312
Dorn, M.W., 180
Dower, J.F., 128
Dowton, M.W., 2255
Drenner, R.W., 2087
Drinkwater, K.F., 2548
Duffy, W.G., 15
Duthie, H.C., 1443
Dutil, J.-D., 788, 1591
Ehrman, J., 2464
Ehtisham, A., 1149
Elliott, J.K., 626
Elliott, S.R., S267
Ellis, N., 2393
Ericson, G., 815
Erkinaro, J., 2266
Essington, T.E., 2310
Estoup, A., 715
Evans, R.D., 909
Evans, S.D., 781
Faber, M.J., 639
Fahrig, L., 76
Fanslow, D.L., 2402
Faure, E., 2341
Fausch, K.D., S218, S303
Fee, E.J., 544
Fend, S.V., 1051
Ferguson, A., 358, 2011
Ferguson, M.M., 1553
Ferreri, C.P., S191
Fjeld, E., 1512
Fleischman, S.J., 2492
Fleming, I.A., S59, S303
Folt, C.L., 116, S1, S9, S288
Foote, C.J., 1524, 2097
Forsgren, H.L., S303
Fournier, D.A., 2105
Fox, M.G., 737
Fransen, B.R., 1909
Franzin, W., 544
Friedland, K.D., 1158, S119, S312
Fryer, R.J., 1632
Fukushima, M., 618
Furgal, J.A., 726
Gagnon, M.M., 1068
Galgani, F., 597
Gallo, K.L., 2087
Gao, Y., 1798
Garcia de Leaniz, C., S312
Garnier-Laplace, J., 999
Garvey, J.E., 2414
Geaghan, J.P., 1328
Gephard, S.R., S281
Gerow, K.G., 1894
Ghan, D., 1338, 1350
Gharbi, K., 715
Gharrett, A.J., 2048
Giberson, D.J., 485
Gibson, J.R., S312
Gilles, A., 2341
Gillis, D.M., 37
Gilmour, C.C., 835
Girard, C., 438
Goddard, P.L., 2048
Goering, J.J., 1494
Goldblatt, R., 1878
Good, S.P., 1663, 1674
Gopalan, G., 2572
Gosselin, J.-F., 825
Graham, M.D., 806
Grant, J.W.A., S181, S303
Grant, S.M., 1307, 1317
Grant, W.S., 2539
Gregory, T.R., 1583
Gresham, D., 1220
Grette, G.B., 1395
Griffin, M.C., 539
Gross, M.R., S131, S312
Guderley, H., 788, 1591
Gunn, J.M., 639
Guyomard, R., 715
Haag, W.R., 297
Haas, R.C., 1085
Haas, R.E., 1158
Haffray, P., 715
Hall, B.D., 2036
Hall, R.I., 587, 668
Hamel, J.-F., 239
Hammill, M.O., 423
Hampton, J., 2105
Hansen, L.P., 507, S77, S104
Hansson, S., 2706
Harris, P.D., S247
Hartson, D.J., 2402
Harvey, B.C., 1902
Havens, K.E., 206, 1652
Hawkins, D.K., 2097
He, J., 2518
Hearn, W.S., 199, 1466, 1477, 2001
Hebert, K.P., 2048
Hebert, P.D.N., 1010
Hedgecock, D., 1025
Heino, M., 1971
Helbig, J.A., 2189, 2206
Helfield, J.M., S267
Helser, T.E., 882, 1328
Hendry, A.P., 1387
Henein, K.M., 76
Hensleigh, J.E., 1387
Herlihy, A.T., 1618
Hershberger, W.K., 1946
Hesslein, R.H., 869
Hewitt, L.M., 2078
Higuchi, K., 2464
Hilborn, R., 529, 2067
Hill, A.R., 495
Hinch, S.G., 1821, 1832
Hobæk, A., 1512
Hobday, A.J., 704
Hobson, K.A., 1114, 2601
Hodgson, J.R., 2588
Hodson, P.V., 1068
Hoenig, J.M., 1466, 1477, 2001
Hoffmann, A., 1484
Holen, D.A., 2150
Hontela, A., 438
Hooke, B., 1208
Horne, J.K., 1296
Houlihan, D.F., 2365
Howell, G.D., 1704
Hrabik, T.R., 1364
Hudon, C., 2317
Hudson, J., 1503
Hughes, R.M., 1618
Huot, J., 825
Hurlbut, T., 2274
Hurley, J.P., 835
Hurst, T.P., 1122, 2709
Huryn, A.D., 1784, S201
Huse, G., 631
Hutchings, J.A., S22, S48
Hyatt, K.D., 1338, 1350
Imsland, A.K., 770
Ing, K.K., 2188

Ishida, Y., 937, 1996
Iverson, S.J., 1378
Iwamoto, R.N., 1484
Jacobson, L.D., 2455
James-Pirri, M.-J., 2436
Janssen, C., 2221
Janssens de Bisthoven, L., 688
Järvinen, M., 2562
Jenkins, T.M., Jr., 2478
Jensen, A.L., 353
Johannsson, O.E., 2187
Johnson, P.D., 1564
Johnson, T.B., 1273
Johnston, N.T., 2425
Jones, M.E.B., 364, S22
Jones, M.L., 2161
Jónsdóttir, O.D.B., 770
Jørgensen, L., 2266
Jørgensen, T., 900
Jourd'heuil, L., 999
Juanes, F., 1695
Karbe, L., 328, 1997
Kaufmann, P.R., 1618
Keeley, E.R., S181
Kelly, J.E., 781
Kerr, S.R., 1378
Kidd, K.A., 869
Kincaid, T.M., 1618
King, J.R., 1999
Kinnison, M.T., 554, 1946
Kirkwood, G.P., 2642
Kirsch, P.E., 1378
Kitchell, J.F., 1273, 2588
Kjesbu, O.S., 900, 1766
Kline, T.C., Jr., 1494
Klotz, R.L., 1228
Knoechel, R., 230
Knyf, M., 1798
Kobayashi, T., 1864
Kocik, J.F., S191
Korman, J., 2117
Korver, R.M., 2161
Krabbenhoft, D.P., 835
Kratz, K., 2478
Kreutzweiser, D.P., 639
Kuhnlein, U., 1104
Laberge, C., 63
Lacroix, G.L., 2117
Lady, J.M., 2580
Lambert, Y., 788
Lang, G.A., 2402
Lange, U., 328, 1997
Lapointe, M.F., 2503
Larsen, D.P., 1618
Larsson, P., 1926
Lasenby, D.C., 909
Lassus, P., 597
Lathrop, R.C., 1169
Lawson, P.W., 2383
Leavitt, P.R., 668
Lecomte, F., 2662
Leggett, W.C., 128, 626
Leland, H.V., 1051
Lester, N.P., 2161
Lewis, A.G., 1878
Li, G., 1025
Limburg, K.E., 431
Lindegaard, C., 1093
Lindesjöö, E., 815
Link, M.R., 1408
Linton, T.K., 576, 1534
Litvak, M.K., 1871
Lizamore, S., 1220
Lonergan, S.P., 2150
Lonzarich, D.G., 2141
Lonzarich, M.R.E., 2141
Lörtscher, M., 2341
Louda, J.W., 206
Lougheed, V.L., 150, 1189
Lowe, R.L., 1043
Lowerre, J.M., 2224
Lowerre-Barbieri, S.K., 2224
Lozano, S.J., 2402
Lupiáñez, J.A., 649
Lymburner, D.J., 495
Ma, Y., 900
MacDonald, M.M., 2150
Mackas, D.L., 1878
Mackie, G.L., 1131
MacLeod, N.A., 1919
Madenjian, C.P., 1085
Madon, S.P., 401, 2058
Magnuson, J.J., 1364, 1573
Maguire, J.-J., 1545
Mahon, R., 1704
Mallory, M.L., 63
Mangel, M., 1179
Marchand, F., 796
Margolis, L., 977
Marmorek, D.R., 2117
Marschall, E.A., S48
Marshall, C.T., 1766
Marshall, R.P., 1983
Marteinsdottir, G., 1372
Martin, S., 1264
Marty, G.D., 2300
Marzolf, E.R., 1786
Mason, D.M., 1273
Mather, M.E., S1, S232, S288
Matthews, M.A., 2011
Maule, A.G., 1599
Maynou, F., 262
Mazumder, A., 1652
McAllister, M.K., 2622, 2642
McCafferty, D.J., 845
McConnaha, W.E., 2178
McCormick, S.D., S77, S281
McDonald, D.G., 1198, 1208, 1534
McFarlane, W.J., 1198, 1208
McGeer, J.C., 2447
McGinnity, P., 358
McHenry, M.L., 1395
McIntosh, A.R., 1954
McKinley, R.S., 682
McLain, A.S., 1364
McLaughlin, R.L., 853
McMahon, R.F., 1564
McMenemy, J., S288
McNicol, D.K., 63
McPhail, J.D., 1338, 1350
Measures, L.N., 825
Meekan, M.G., 1663, 1674
Mercier, A., 239
Mertz, G., 478, 2355
Mesa, M.G., 1599
Metcalfe, N.B., S48, S93
Methven, D.A., 1430, 2283
Meyers, T.R., 2300
Miller, K.A., 2255
Miller, R., 54
Milligan, C.L., 1198, 1208
Miner, J.G., 1043
Mittelbach, G.G., 1454
Moles, A., 605
Monaco, M.E., 1704
Mooij, W.M., 451
Moore, A., S288
Morgan, I.J., 576
Morin, R., 2548
Mort, M.E., 861
Motycka, M., 987
Muir, D.C.G., 544, 869
Mulholland, P.J., 1786
Mullins, C.C., 246
Munkittrick, K.R., 2078
Murata, S., 1864
Murdoch, R.C., 1682
Myers, R.A., 423, 478, 2329, 2355
Nævdal, G., 770
Nagasawa, K., 937, 1996
Naiman, R.J., S267, S288
Nalepa, T.F., 2402
Näslund, I., 1034
Néji, H., 2019
Newbury, R., S312
Nibbelink, N.P., 387
Nickelson, T.E., 2383
Nielsen, J.L., S145, S312
Niemelä, E., 2266
Nislow, K.H., 116, S9
Noakes, D.L.G., 853
Noguchi, G.E., 1085
Nonacs, P., 1179
Norcross, B.L., 605
Nordwall, F., 1034
Norton, S.A., 1512
Novinger, D.C., 1894
Numachi, K.-i., 1864
O'Boyle, R.N., 1704
O'Connell, M.F., 246

Okada, N., 1864
Okazaki, T., 1864
Okla, L., 1926
Ollevier, F., 688
Owen, S.F., 2365
Page, M.J., 1682
Panuska, J.C., 1169
Parker, B.R., 170
Parkinson, E.A., 2425
Parnell, I., 2117
Paron, D.G., 2310
Parren, P., 688
Parrish, D.L., S1, S161, S281
Paterson, M.J., 544
Peake, S., 682
Pelletier, D., 788, 2672
Pelletier, É., 239
Pepin, P., 128, 2189, 2206
Peragón, J., 649
Perry, R.W., 781
Persoone, G., 2221
Persson, L., 1454
Peterman, R.M., 37, 86, 1408, 2127, 2503, 2710
Piet, G.J., 1842
Pigeon, D., 1739
Pipp, E., 1443
Plisetskaya, E.M., 2376
Poe, T.P., 1599
Poff, N.L., S48, S201
Polacheck, T., 1477
Pollard, H.G., 639
Pollock, K.H., 199, 1466, 1477, 2001
Poole, W.R., 2011
Pope, S.E., 76
Post, D.M., 2588
Post, J.R., 2425
Postma, J.F., 688
Power, M.E., S9, S312
Power, M.V., 143
Prepas, E.E., 2292
Prowse, T.D., S161, S303
Puel, O., 597
Pyper, B.J., 2127, 2503, 2710
Quinlan, R., 587
Quinn, T.J., 618
Quinn, T.P., 554, 1946, S48, S77, S104
Rahel, F.J., 1894
Rand, P.S., 307, 318, 1821, 1832
Rasmussen, J.B., 1759
Rebert, S.D., 99
Reddin, D.G., 1158
Reeves, G.H., S281
Reid, K., 845
Reid, S.D., 1534
Reinert, T.R., 539
Reisenbichler, R.R., 1387
Rempel, L.L., 893
Rennie, M.J., 2365
Reynolds, L., 1618
Ricciardi, A., 1759
Rice, S.D., 2300
Richards, L.J., 515, 949, 1545
Robb, C.A., 86
Robichaud, G., 262
Robins, C.M., 1645
Roff, D.A., S48
Rognerud, S., 1512
Rondorf, D.W., 781
Rose, G.A., 76
Rosenberg, B., 544
Rosenberg, D.M., 2036
Rott, E., 1443
Roy, S., S312
Russ, G.R., 917
Ruzzante, D.E., 1
Ryan, D.A.J., 1663, 1674
Saari, A., 2266
Sabater, F., 1938
Saborowski, R., 328, 1997
Sainte-Marie, B., 459, 1104
Salonen, K., 2562
SanCristobal, M., 715
Sanderson, S.L., 861
Sarnelle, O., 2478
Saunders, R.L., S48, S77
Scharf, F.S., 1695
Schell, D.M., 2601
Schindler, D.W., 170, 869
Schleen, L.P., 2078
Schlosser, I.J., S303
Schneider, D.C., 1430, 2283
Schneider, D.W., 401
Schnute, J.T., 515, 949
Schreck, C.B., 1599
Schrouder, K.S., 1085
Schultz, E.T., 1149
Schwarcz, H.P., 1798
Schwartz, W.J., 987
Schwarz, C.J., 281
Scott, I.M., 2078
Scribner, K.T., 1748
Seandel, M., 116
Seeb, L.W., 1748
Sellers, T.J., 170
Servos, M.R., 2078
Sévigny, J.-M., 1104
Shaw, P.A., 658
Shaw, W., 958
Shearer, K.D., 2376
Sheehy, M., 925
Shimizu, N., 1158
Shott, E., 1395
Shustov, Y., 2266
Shuter, B.J., 1999, 2161, 2188
Sibert, J.R., 2105
Siebers, D., 328, 1997
Silverstein, J.T., 2376
Sinclair, A.F., 1248
Sinclair, M., 1704
Sirois, P., 2662
Skalski, J.R., 761, 1484, 2580
Skotvold, T., 1512
Smedbol, R.K., 2283
Smith, B.D., 1236
Smith, D.G., 893
Smith, J.D., 2087
Smith, P.E., 1179
Smith, R.E.H., 726
Smith, R.J.F., 611
Smith, S.G., 1484
Smoker, W.W., 618, 2048
Smokorowski, K.E., 909
Smol, J.P., 587
Solemdal, P., 1766
Soleng, A., 507
Soranno, P.A., 1169
Sorenson, P.W., 2310
Sparks, R.E., 401
Spearman, W.J., 1748
Starr, M., 262
Starr, P., 529
Stein, R.A., 2414
Steingrímsson, S.Ó., S181
Steinman, A.D., 206, 1786
Stemberger, R.S., 339
Stenson, G.B., 423
Stevens, E.D., 2028
Stewart, D.J., 307, 318, 2518
Stewart, T.W., 1043
Stobo, W.T., 423
Stockwell, J.D., 2187
Stoeckel, J.A., 401
Stow, C.A., 1169
Stratoudakis, Y., 1632
Sullivan, P.J., 99
Sutterlin, A., 2028
Swain, D.P., 2548
Taggart, C.T., 364
Takasaki, N., 1864
Taniguchi, Y., 1894
Taylor, C.G., 281
Taylor, R., 845
Taylor, W.D., 726
Therriault, J.-C., 262
Thomas, R.E., 2300
Thompson, C.E., 2011
Thompson, D.G., 639
Thorarinsson, K., 1372
Thorp, J.H., 220
Thronæs, E., 47
Timmermans, K.R., 688
Todd, T.N., 1140
Tonn, W.M., 170
Townsend, C.R., 1954
Trauben, B.K., 2572
Trevorrow, M.V., 1419
Trippel, E.A., 1871
Tufts, B.L., 1208

Ulltang, Ø., 1766
Unwin, M.J., 554, 1946
Urbani, N., 1104
Van Den Avyle, M.J., 539
Van Der Kraak, G.J., 2078
van Nes, E.H., 451
van Weerd, J.H., 2365
Ventelä, A.M., 1961
Verspoor, E., S153
Vignaux, G.A., 1220
Vignaux, M., 1220
Vinebrooke, R.D., 668, 806
Vis, C., 1078
Vray, F., 999
Wada, T., 2455
Wahle, R.A., 2436
Walker, T.R., 845
Wallin, J., 539
Walls, M., 1961
Walsh, M., 2608
Walsh, P.J., 576
Walter, J.K., 1909
Walters, C.J., 2503, 2533, 2691
Wang, F., 2221
Wang, Y.-G., 397, 1645, 2393
Ward, B., 2533
Warren, M.L., Jr., 297, 2141
Watt, W.D., 2117
Watters, G., 704
Watzin, M.C., 28
Wehr, J.D., 2150
Welch, D.W., 937, 1996
Welch, H.E., 1114
Whiteside, M.C., 1093
Wiens, A.P., 2036
Williams, J.G., 1484
Wilson, C.C., 1010
Wilson, W.J., 1494
Wilzbach, M.A., S288
Winfree, N.M., 206
Wing, S.R., 1236
Wipfli, M.S., 1503
Wood, C.M., 576, 1534, 1583, 2447
Wright, R.A., 2414
Wroblewski, J.S., 2283
Wu, L., 2572
Yan, N.D., 1573
Yaragina, N.A., 1766
Young, R.G., 1784
Youngson, A.F., 1158, S153, S288
Zabel, R.W., 658
Zadworny, D., 1104
Zeldis, J.R., 1682
Zeller, D.C., 917
Zimmerman, A.P., 1999
Zwanenburg, K.C.T., 1704

The index and/or table of contents has been removed and photographed separately within this volume year.

For roll film users, this information for the current volume year is at the beginning of the microfilm. For a prior year volume, this information is at the end of the microfilm.

For microfiche users, the index and/or contents is contained on a separate fiche.

CANADIAN FEDERATION OF BIOLOGICAL SOCIETIES
42ND ANNUAL MEETING

FÉDÉRATION CANADIENNE DES SOCIÉTÉS DE BIOLOGIE
42e CONGRÈS ANNUEL

BRODIE CENTER
WINNIPEG, MANITOBA
JUNE 2 - 5, 1999

THEME I – CARDIOVASCULAR DISEASE

Plenary Lecturer
Dr. Litsa Kranias, University of Cincinnati
Genetically Engineered Mouse Models: Novel Insights into Cardiac Regulatory Mechanisms

Symposia: Signaling in the Heart in Health and Disease
Molecular Origins of Cardiovascular Disease
Biophysical Insights into Cardiovascular Complexity

THEME II –HUMAN GENETICS, DIABETES AND ABORIGINAL HEALTH

PMAC Lecturer
Dr. Emöke Szathmáry, University of Manitoba
Human Genetics, Diabetes and Aboriginal Health

Symposia: A Broader Perspective on Diabetes Focusing on the Aboriginal Community
Genetic Factors in Cellular and Organismal Aging

THEME III –DEVELOPMENTAL BIOLOGY

PMAC Lecturer
Dr. James Davie, University of Manitoba
Developmental Biology

Symposia: Regulation and Function of Heat Shock Protein in Developing, Maturing, and Dying Cells
Neonatal Nutrition and Metabolism

THEME IV – MOTOR CONTROL, NEUROSCIENCE, HUMAN PERFORMANCE

PMAC Lecturer
Dr. David Wasserman, Vanderbilt University
Motor Control, Neuroscience, Human Performance

OTHER

Trace Elements and Molecular Mechanisms of Disease
Communicating Nutrition: From Science to Behavioral Change
Non-Invasive Methods in Diagnosis
Glycobiology

CFBS OPEN SCIENCE POLICY FORUM

Abstract Deadline:
March 1, 1999

For further information:
Pour plus d'information:

CANADIAN FEDERATION OF BIOLOGICAL SOCIETIES
104 - 1750 Courtwood Cres., Ottawa, Ontario K2C 2B5
Tel: (613) 225-8889 Fax: (613) 225-9621 E-Mail cfbs@igs.net
Web site: www.fermentas.com/cfbs

M.K. McAllister and G.P. Kirkwood	**2642–2661**	Using Bayesian decision analysis to help achieve a precautionary approach for managing developing fisheries
Pascal Sirois, Frédéric Lecomte, and Julian J. Dodson	**2662–2671**	An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae
PERSPECTIVES		PERSPECTIVES
D. Pelletier	**2672–2690**	Intercalibration of research survey vessels in fisheries: a review and an application
Carl Walters	**2691–2705**	Evaluation of quota management policies for developing fisheries
DISCUSSION		DISCUSSION
Sture Hansson	**2706–2707**	Methods of studying fish feeding: a comment
Enric Cortés	**2708**	Methods of studying fish feeding: reply
ERRATA		ERRATA
Thomas P. Hurst and David O. Conover	**2709**	Erratum: Winter mortality of young-of-the-year Hudson River striped bass (*Morone saxatilis*): size-dependent patterns and effects on recruitment
Brian J. Pyper and Randall M. Peterman	**2710**	Erratum: Comparison of methods to account for autocorrelation in correlation analyses of fish data

Author index for Volume 55 / Index des auteurs pour le volume 55 **AI-1**
Contents for Volume 55 / Sommaire pour le volume 55 **C-1**

National Research Council Canada
Ottawa, Canada K1A 0R6

Conseil national de recherches Canada
Ottawa, Canada K1A 0R6

Postage paid at Ottawa
Publications mail
Registration No. 1240579

Port payé à Ottawa
Poste-publication
Enregistration n° 1240579

Canadian Journal of Fisheries and Aquatic Sciences

Volume 55, Number 12, December 1998

Journal canadien des sciences halieutiques et aquatiques

Volume 55, numéro 12, décembre 1998

RAPID COMMUNICATION

Carl Walters and Bruce Ward **2533–2538** Is solar radiation responsible for declines in marine survival rates of anadromous salmonids that rear in small streams?

ARTICLES

W. Stewart Grant, A.-M. Clark, and Brian W. Bowen **2539–2547** Why restriction fragment length polymorphism analysis of mitochondrial DNA failed to resolve sardine (*Sardinops*) biogeography: insights from mitochondrial DNA cytochrome *b* sequences

D.P. Swain, G.A. Chouinard, R. Morin, and K.F. Drinkwater **2548–2561** Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence

Marko Järvinen and Kalevi Salonen **2562–2571** Influence of changing food web structure on nutrient limitation of phytoplankton in a highly humic lake

Gouthaman Gopalan, David A. Culver, Lin Wu, and Bruce K. Trauben **2572–2579** Effects of recent ecosystem changes on the recruitment of young-of-the-year fish in western Lake Erie

James M. Lady and John R. Skalski **2580–2587** Estimators of stream residence time of Pacific salmon (*Oncorhynchus* spp.) based on release–recapture data

David M. Post, James F. Kitchell, and James R. Hodgson **2588–2600** Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake

Keith A. Hobson and Don M. Schell **2601–2607** Stable carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*)

N.H. Augustin, D.L. Borchers, E.D. Clarke, S.T. Buckland, and M. Walsh **2608–2621** Spatiotemporal modelling for the annual egg production method of stock assessment using generalized additive models

Murdoch K. McAllister **2622–2641** Modeling the effects of fish migration on bias and variance in area-swept estimates of biomass: a vector-based approach

Continued on inside back cover / Suite au verso

Canada

Printed in Canada by / Imprimé au Canada par
University of Toronto Press Inc.
Typesetting by / Typographie par
NRC Research Press / Presses scientifiques du CNRC

0706-652X(199812)55:12;1-N